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DEEP-SEA CRYPTOBRANCH DORID NUDIBRANCHS (MOLLUSCA, OPISTHOBRANCHIA) FROM THE TROPICAL WEST PACIFIC, WITH DESCRIPTIONS OF TWO NEW GENERA AND EIGHTEEN NEW SPECIES

Ángel Valdés

Department of Invertebrate Zoology and Geology, California Academy of Sciences,
Golden Gate Park, San Francisco, CA 94118, U.S.A.; avaldes@calacademy.org

ABSTRACT

The study of a large collection of cryptobranch dorid nudibranchs from deep waters in New Caledonia and the Philippines revealed the presence of *Austrodoris kerguelenensis* (Bergh, 1884); 18 new species belonging to the genera *Cadlina*, *Austrodoris, Geitodoris, Discodoris, Peltodoris, Paradoris*, *Diaulula, Rostanga*, *Sclerodoris, Baptodoris* and *Dendrodoris;* and two previously undescribed genera, *Goslineria* and *Pharodoris.* The anatomy of all these species, including the digestive, reproductive, and nervous system, are studied in detail.

All these species are clearly distinguishable from other members of their genera. Most of the species have a pale, simple background coloration, and two of them lack eyes. Both characteristics seem to be adaptations to living in deep waters. Other deep-water Atlantic and Pacific species of dorid nudibranchs have similar adaptations. The two new genera are characterized by the presence of large copulatory spines, numerous flexible spines in *Goslineria,* and two solid, bifid spines in *Pharodoris.* No other cryptobranch dorid genera previously described have similar copulatory spines.

Some of the species here described belong to genera previously reported from cold or temperate waters, such as *Austrodoris, Cadlina* and *Diaulula.* Most of the species belong to genera that are widespread in either cold, temperate or tropical waters (*Rostanga, Paradoris, Geitodoris* and *Baptodoris*), and only two belong to exclusively tropical genera (*Sclerodoris* and *Dendrodoris*). Vicariant events and vertical dispersal could explain the processes of speciation and the origin of these deep-water species.

Key words: Mollusca, Nudibranchia, Doridina, deep-water, Pacific Ocean.

INTRODUCTION

In contrast to other groups of mollusks with a well-documented deep-sea occurrence and numerous described deep-water species, very little is known about deep-sea opisthobranch mollusks, and particularly about deep-sea dorid nudibranchs.

To date, only three papers dealing with deep Atlantic species of dorids have been published. The first is Bouchet (1977), who described five new species and a new genus of cryptobranch dorids, including phyllidiids, from the northeast Atlantic. Later, Valdés & Ortea (1996) described two new deep-sea phyllidiids, also from the northeast Atlantic, and Valdés & Bouchet (1998a) described an abyssal new genus of Corambidae from the Norwegian Sea.

The first report on deep-water Indo-Pacific dorids was Bergh's (1884) description of *Bathydoris abyssorum* Bergh, 1884, collected at 4,435 m depth off New Ireland, Papua New Guinea, during the Challenger Expedition. Bergh (1884) also described *Archidoris australis* Bergh, 1884, collected off the Kerguelen Island at 173 m depth. Other dorids studied in that paper were collected from shallow water. Subsequently, García et al. (1993) reported *Austrodoris kerguelenensis* (Bergh, 1884) from Antarctic deep waters. The genus *Bathydoris* is collected from deep or cold shallow waters, and it is the only genus of dorid nudibranchs that is consistently known from the deep sea (Wägele, 1989; Baranets, 1993; Valdés & Bertsch, 2000).

There had not been a significant collecting effort of deep-sea opisthobranchs in the Indo-Pacific until the French Musorstom Expeditions. Three papers on dorid nudibranchs have been produced from the material collected in these expeditions: Valdés (2001) described 12 new species of Phyllidiidae (genera *Phyllidia* and *Phyllidiopsis*) from deep waters around New Caledonia; Valdés & Gosliner (in press) described four new species and a new genus of caryophyllidia-bearing dorids from New Caledonia and the Philippines; and Fahey & Gosliner (2000) described three new species of the genus *Halgerda* from these two areas and from Fiji.

Despite this recent proliferation of papers, there are still numerous genera and families of dorids never reported from the deep sea. The present paper deals with the bulk of the collection of cryptobranch dorids collected during the Musorstom Expeditions; it constitutes the first attempt to describe in detail the deep-water biodiversity of Indo-Pacific dorid nudibranchs.

MATERIALS AND METHODS

The material examined was collected during several French scientific expeditions to the southwest Pacific Ocean (Fig. 1) and the Philippines between the years 1981 and 1994, organized by the Institut de Recherche pour le Développement (IRD, formerly ORSTOM) and the Muséum National d'Histoire Naturelle, Paris. All specimens, including the type material, are deposited at the Laboratoire de Biologie des Invertébrés Marins et Malacologie of the Muséum National d'Histoire Naturelle, Paris (MNHN), the Department of Invertebrate Zoology and Geology of the California Academy of Sciences (CASIZ) and the Australian Museum, Sydney (AM). Registration numbers are not used in MNHN, and individual lots and specimens are identified by the unique combination of the station number and cruise acronym.

Descriptions of living animals are based on photographs or notes by collectors. All specimens available were dissected, and morphological examination was facilitated by making a dorsal incision. The internal features were examined and drawn using a dissecting microscope with a camera lucida. A portion of the mantle was critical-point dried for the Scanning Electron Microscope (SEM). Special attention was paid to the morphology of the reproductive system, digestive system, and central nervous system. The numbering of the nerves in the central nervous system was determined according to their relative position on the ganglia. The buccal mass was removed and dissolved in 10% sodium hydroxide until the radula was isolated from the surrounding tissue. The radula was then rinsed in water, dried, and mounted for examination with the SEM.

DESCRIPTIONS

Genus *Cadlina* Bergh, 1879
Type Species: *Doris repanda* Alder & Hancock, 1842, by monotypy [= *Cadlina laevis* (Linnaeus, 1767)].

Cadlina abyssicola Valdés, new species
(Figs. 2A, 3, 4)

Material Examined

HOLOTYPE: East of New Caledonia, Bathus 1 Expedition, stn. CP670 (20°54'S, 165°53'E), 394-397 m, 14 March 1993, 17 mm preserved length, leg. P. Bouchet and B. Richer de Forges (MNHN).

PARATYPES: New Caledonia, Musorstom 4 Expedition, stn. DW222 (22°38'S, 167°37'E), 535-560 m, 29 September 1985, one specimen 13 mm preserved length, dissected, leg. P. Bouchet and B. Richer de Forges (MNHN); stn. CC247 (22°09'S, 167°13'E), 435-460 m, 4 October 1985, one specimen 20 mm preserved length, dissected, leg. P. Bouchet and B. Richer de Forges (MNHN). Île des Pins, south of New Caledonia, SMIB 8 Expedition, stn. DW195 (22°59'S, 168°21'E), 508-514 m, 1 February 1993, one specimen 20 mm preserved length, dissected, leg. P. Bouchet and B. Richer de Forges (MNHN). South of New Caledonia, Bathus 2 Expedition, stn. CP735 (23°02'S, 166°56'E), 530-570 m, 13 May 1993, one specimen 15 mm preserved length, leg. P. Bouchet and B. Richer de Forges (MNHN). Norfolk Ridge, New Caledonia, Bathus 3 Expedition, stn. CP831 (23°04'S, 166°56'E), 650-658 m, 30 November 1993, one specimen 13 mm preserved length, leg. P. Bouchet, B. Richer de Forges and A. Warén (MNHN); stn. CP846 (23°03'S, 166°58'E), 500-514 m, 1 December 1993, one specimen 14 mm preserved length, leg. P. Bouchet, B. Richer de Forges and A. Warén (MNHN); stn. CP847 (23°03'S, 166°58'E), 405-411 m, 1 December 1993, one specimen 15 mm preserved length, leg. P. Bouchet, B. Richer de Forges and A. Warén (MNHN). Southwest of New Caledonia, Halipro 1 Expedition, stn. CP868 (21°14'S, 165°55'E), 430-455 m, 23 March 1994, one specimen 12 mm preserved length, leg. B. Richer de Forges (MNHN); stn. CP869 (21°14'S, 165°55'E), 450-490 m, 23 March 1994, three specimens 11-16 mm preserved length, leg. B. Richer de Forges (CASIZ 121095). North of New Caledonia,

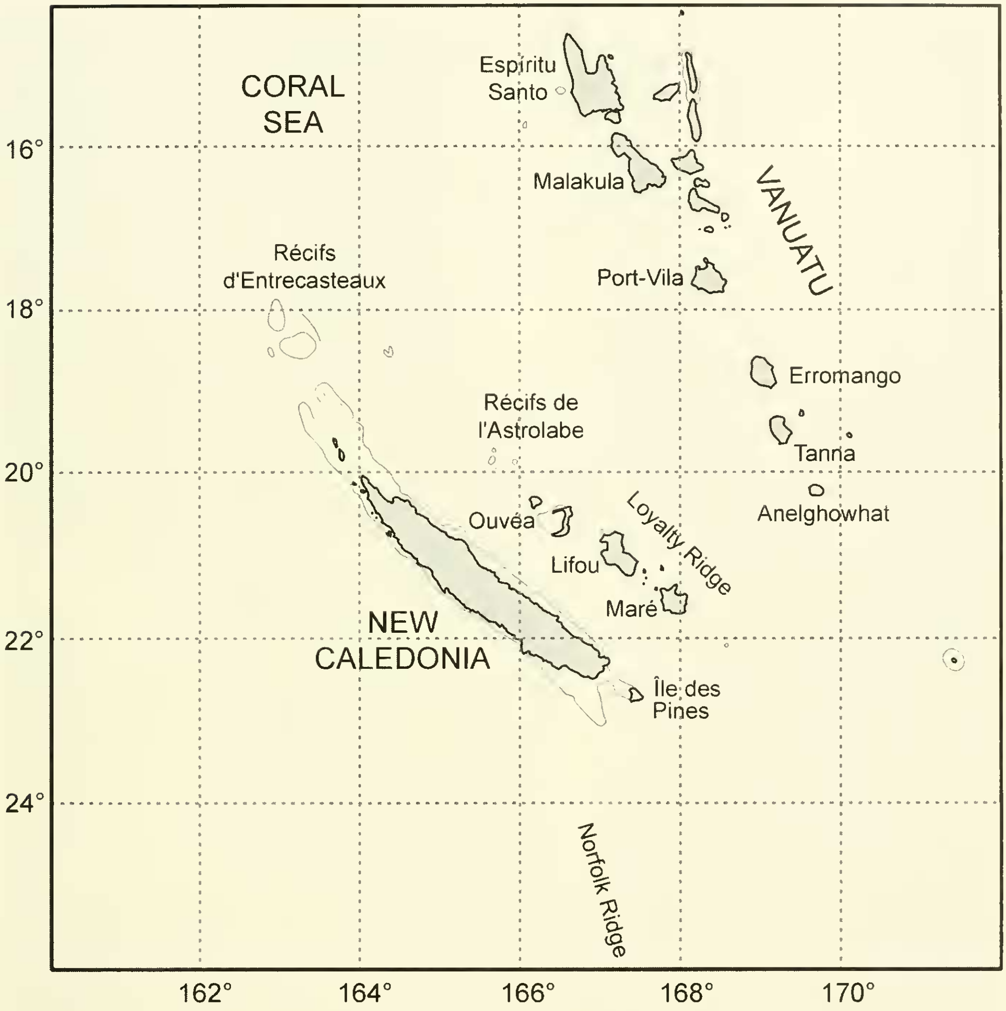

FIG. 1. Map of the New Caledonia region, where most of the samples were collected.

Bathus 4 Expedition, stn. DW941 (19°02′S, 163°27′E), 270 m, 8 August 1994, one specimen 14 mm preserved length, leg. B. Métivier and B. Richer de Forges (MNHN).

External Morphology

The body is somewhat elevated, oval (Fig. 2A). The dorsum is covered with simple, conical tubercles. Some of them, more sparsely arranged, are much larger than the others. There are several, simple and isolated mantle glands around the mantle margin. The perfoliate rhinophores are composed of 30 lamellae. There are seven bipinnate branchial leaves. Ventrally, the oral tentacles are short and grooved (Fig. 3F). The anterior border of the foot is grooved but not notched. The mantle margin is about as wide as the foot.

Based on the field notes, the background color of the living animals is uniformly white to cream. The apices of the larger tubercles are yellow. The rhinophores and gill have the same color as the dorsum. The mantle glands are yellow in the preserved specimens.

Anatomy

The posterior end of the oral tube has two strong retractor muscles (Fig. 3E), which are

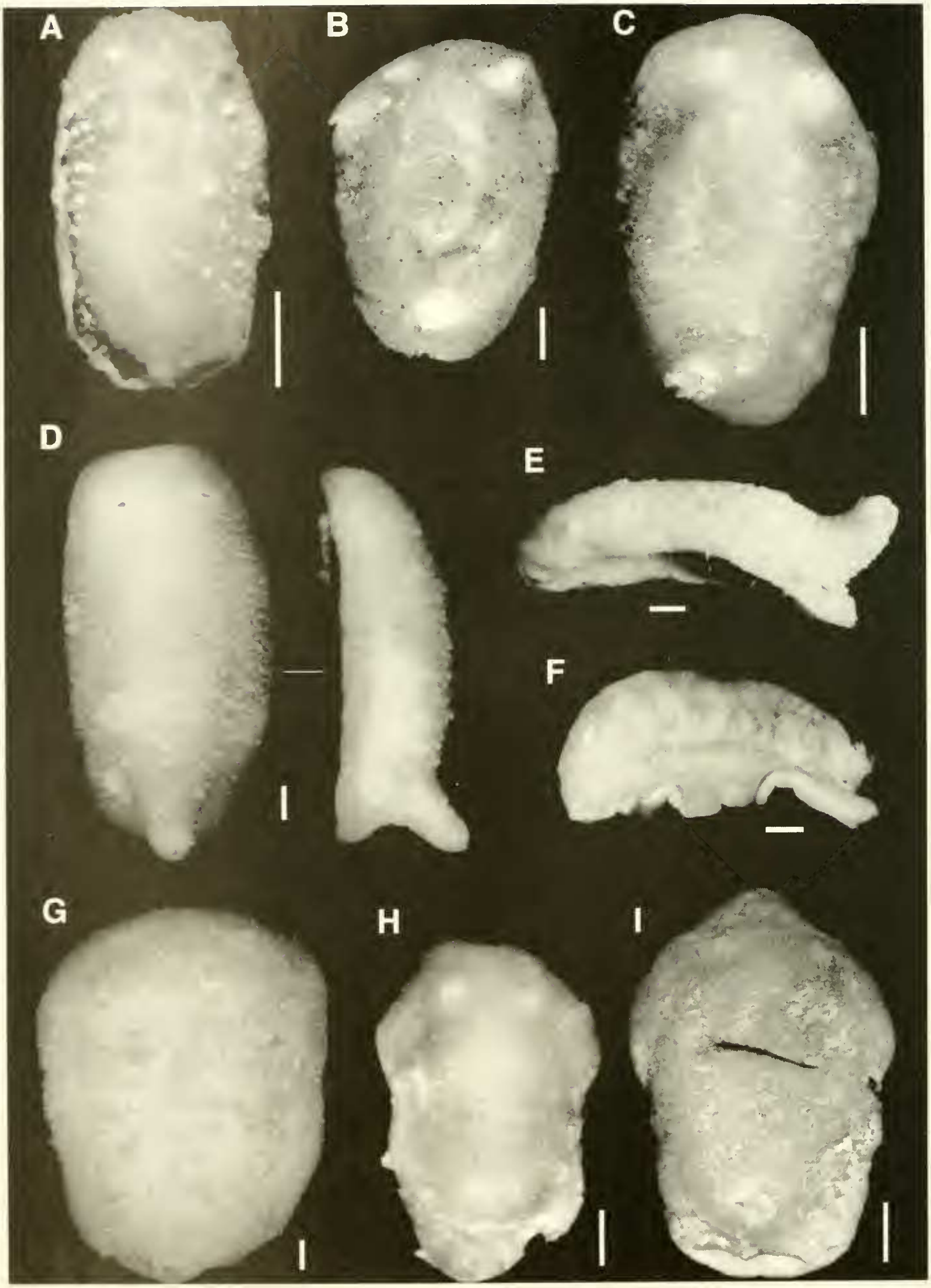

FIG. 2. Preserved specimens. A. *Cadlina abyssicola,* new species, paratype from Musorstom 4 (stn. CC247); scale bar = 5 mm. B. *Austrodoris kerguelenensis,* Biocal (stn. DW33); scale bar = 2 mm. C. *Austrodoris caeca,* new species, paratype from Halipro 1 (stn. CH876); scale bar = 5 mm. D. *Pharodoris diaphora,* new species, holotype; scale bar = 2 mm. E. *Pharodoris philippinensis,* new species, holotype; scale bar = 2 mm. F. *Austrodoris laboutei,* new species, holotype; scale bar = 2 mm. G. *Geitodoris pallida,* new species, holotype; scale bar = 1 mm. H. *Discodoris achroma,* new species, paratype from Bathus 3 (stn. CP832); scale bar = 2 mm. I. *Discodoris* sp.; scale bar = 10 mm.

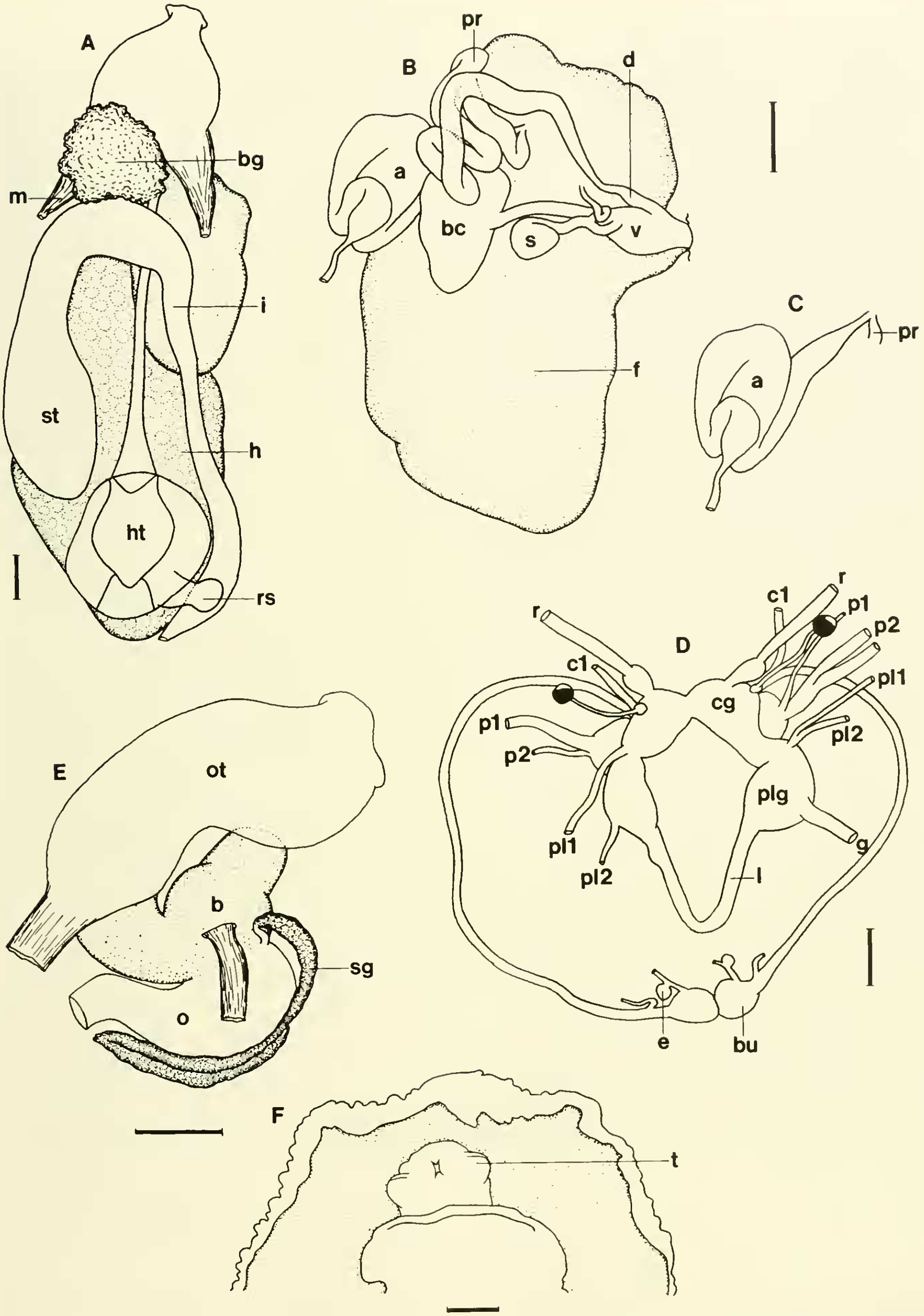

FIG. 3. *Cadlina abyssicola,* new species, paratype from SMIB 8 (stn. DW195). A. Dorsal view of the anatomy; scale bar = 1 mm. B. Reproductive system; scale bar = 1 mm. C. Detail of the ampulla and prostate connection; scale bar = 1 mm. D. Central nervous system; scale bar = 0.5 mm. E. Anterior portion of the digestive system; scale bar = 1 mm. F. Mouth area; scale bar = 1 mm. Abbreviations: a, ampulla; b, buccal bulb; bc, bursa copulatrix; bg, blood gland; bu, buccal ganglion; c, cerebral nerve; cg, cerebral ganglion; d, deferent duct; e, esophageal ganglion; f, female glands; g, genital nerve; h, hermaphrodite and digestive glands; ht, heart; i, intestine; l, visceral loop; m, retractor muscle; o, esophagus; ot, oral tube; p, pedal nerve; pl, pleural nerve; plg, pleural ganglion; pr, prostate; r, rhinophoral nerve; rs, renal syrinx; s, seminal receptacle; sg, salivary gland; st, stomach; t, oral tentacle; v, vagina.

attached to the body wall. The small, oval, muscular buccal bulb has two additional muscles. Two long salivary glands connect to the buccal bulb at the sides of the esophageal junction. The buccal bulb is one-half as long as the oral tube. The jaws consist of numerous thin, unicuspid elements about 20 μm long (Fig. 4D). The radular formula is 59 × (45.1.45) in a 20 mm preserved length specimen. The rachidian teeth have 4–5 elongate denticles, none of them clearly larger than the others (Fig. 4A). The inner lateral teeth are hamate, having a single cusp and a series of denticles. The innermost lateral tooth has 3–4 short denticles on the inner side and 6–7 short, blunt denticles on the outer side. The following teeth have 7–10 blunt denticles only on the outer side. The teeth increase in size gradually towards the medial portion of the half-row. The mid-lateral teeth are hamate, with a long cusp, and they lack denticles (Fig. 4B). The outermost teeth have 10–12 small denticles (Fig. 4C). The esophagus is long and connects directly to the digestive gland.

The ampulla is long and convoluted; it narrows into the gonoduct, which branches into a short oviduct and the prostate (Fig. 3C). The oviduct enters the female glands near the center of the mass. The prostate is tubular and elongate (Fig. 3B); it narrows and expands again into the short deferent duct. The deferent duct opens into a common atrium with the vagina. The penis is unarmed. The vagina is long and wide. At its proximal end, the vagina connects to the large, irregular bursa copulatrix. From the distal end of the vagina, near the opening, a short duct connects to the seminal receptacle and the uterine duct. The bursa copulatrix is about ten times larger than the seminal receptacle.

In the central nervous system (Fig. 3D), the cerebral and pleural ganglia appear to be partially fused and distinct from the pedal ganglia. There are four cerebral nerves leading from each cerebral ganglion, and two pleural nerves lead from each pleural ganglion. The buccal ganglia lie near the rest of the central nervous system, joined to the cerebral ganglia by two long nerves. Gastroesophageal, rhinophoral, and optical ganglia are present. The pedal ganglia are clearly separated, with two nerves leading from each. The pedal and parapedal commissures are enveloped together with the visceral loop along all their length.

The circulatory system (Fig. 3A) consists of a heart and a single blood gland situated over the central nervous system.

Etymology

From the Ancient Greek *abyssos* (deep) and the Latin *cola* (dweller), in reference to the habitat of this species, used as a noun in apposition.

Remarks

Cadlina abyssicola is clearly distinguishable from other species of the genus. All the species previously described have denticulated mid-lateral teeth (Rudman, 1984), whereas *C. abyssicola* has smooth mid-lateral teeth. Also, species of *Cadlina,* except *Cadlina dubia* Edmunds, 1981, have bifid jaw rodlets (Rudman, 1984), whereas in *C. abyssicola* all of them are simple. *Cadlina dubia,* described from Ghana, differs from *C. abyssicola* in having much shorter radular teeth, all bearing strong denticles (Edmunds, 1981).

Cadlina willani Miller, 1980, from New Zealand, is the species with the closest geographic range to *C. abyssicola*. It is a white species with a mid-dorsal yellow stripe and a yellow band around the mantle margin. It is very different from *C. abyssicola,* which is white with yellow spots. Moreover, the morphology of the radular teeth is very different between these two species. The inner lateral teeth of *C. abyssicola* are narrow and elongate and have 6–7 short denticles on the outer side of the cusp, whereas those of *C. willani* are shorter and have only 3 denticles on the outer side (Miller, 1980). Also, the mid-lateral teeth of *C. abyssicola* are smooth, whereas in *C. willani* the mid-lateral teeth have 7 strong denticles.

Cadlina nigrobranchiata Rudman, 1985, from southern Australia is clearly distinguishable from *C. abyssicola* in having a black gill and black rhinophores (Rudman, 1985). Also, the radular morphology of these two species is very different. The rachidian teeth of *C. nigrobranchiata* are much shorter than those of *C. abyssicola.* Moreover, the mid-lateral teeth of *C. abyssicola* are smooth, whereas in *C. nigrobranchiata* they have several strong denticles.

Schrödl (2000) reviewed the species of *Cadlina* from South America and Antarctica. All of them are clearly distinguishable from *C.*

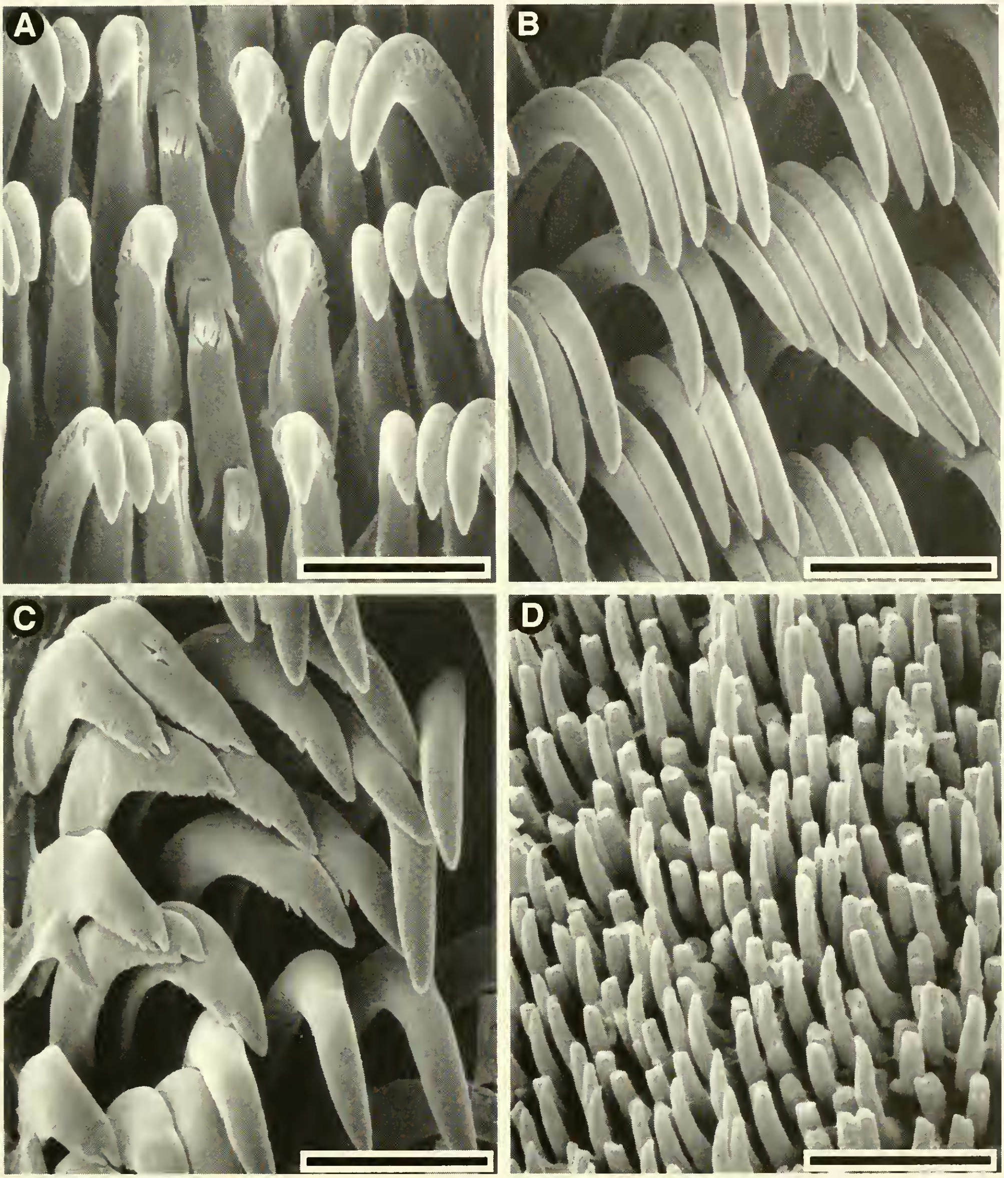

FIG. 4. *Cadlina abyssicola,* new species, paratype from SMIB 8 (stn. DW195). A. Inner lateral teeth; scale bar = 43 μm. B. Mid-lateral teeth; scale bar = 60 μm. C. Outer lateral teeth; scale bar = 43 μm. D. Jaw elements; scale bar = 30μm.

abyssicola in their radular morphology and anatomy. These five species – *Cadlina kerguelensis* Thiele, 1912; *C. sparsa* (Odhner, 1921); *C. magellanica* Odhner, 1926; *C. affinis* Odhner, 1934; *C. georgiensis* Schrödl, 2000 – have denticulate mid-lateral teeth, whereas they are smooth in *C. abyssicola*. In *C. affinis* and *C. magellanica,* the seminal receptacle inserts in the middle of the vagina, in *C. kerguelensis* and *C. sparsa* it inserts near the bursa copulatrix, whereas in *C. georgiensis* and *C. abyssicola* the insertion is closer to the opening of the vagina. However, in *C. abyssicola* the seminal receptacle is more distal than in *C. georgiensis* and it is clearly stalked. In addition, the prostate and the ampulla of *C. abyssicola* appear to be longer than those of *C. georgiensis.*

Cadlina sp. (Fig. 5)

Material Examined

New Caledonia, Biocal Expedition, stn. DW14 (22°47′S, 167°14′E), 440–450 m, 30 August 1985, one specimen 5 mm preserved length, leg. P. Bouchet, B. Métivier and B. Richer de Forges (MNHN).

External Morphology

The body is somewhat elevated, oval. The dorsum is covered with simple, conical tubercles that are evenly arranged. The perfoliate rhinophores are composed of nine lamellae. There are five bipinnate branchial leaves. Ventrally, the oral tentacles are short and grooved. The anterior border of the foot is simple. The mantle margin is wider than the foot.

The color of the living animal is unknown. The preserved specimen is uniformly white to cream. The rhinophores and gill have the same color as the dorsum.

Anatomy

The jaws consist of numerous thin, unicuspid elements about 10 μm long (Fig. 5D). The radular formula is 68 × (19.1.19) in a 5 mm preserved length specimen. The rachidian teeth have a large, single central cusp and 5–6 blunt denticles on each side (Fig. 5A). The inner lateral teeth are wide, hamate, having a single cusp and a series of denticles. These teeth have 2–3 denticles on the inner side and 10–12 elongate denticles on the outer side. The teeth increase in size gradually towards the medial portion of the half-row. The mid-lateral teeth are hamate, with a long cusp and 7–8 large denticles only on the outer side (Fig. 5B). The outermost teeth have 5–11 denticles (Fig. 5C).

The reproductive system of the single specimen collected was immature, so information on the genital morphology is not available.

Remarks

The radular morphology of this species is very distinct from other members of the genus *Cadlina*. The rachidian teeth have a number of small denticles on each side of the central cusp that are not present in any other species previously described (Rudman, 1984)

However, since the color of the living animal is unknown, and the reproductive system of the single specimen collected is immature, I prefer not to name this species until new material becomes available.

Genus *Austrodoris* Odhner, 1926

Type Species: *Archidoris rubescens* Bergh, 1898, by original designation [= *Austrodoris kerguelenensis* (Bergh, 1884)].

Austrodoris kerguelenensis (Bergh, 1884) (Figs. 2B, 6, 7)

Archidoris kerguelenensis Bergh, 1884: 85–89, pl. 1, figs. 1–12.

Austrodoris georgiensis García et al., 1993: 417–421, figs. 1–8, new synonymy herein.

See Wägele (1990, 1993) for a complete list of synonyms.

Material Examined

New Caledonia, Biocal Expedition, stn. DW33 (23°10′S, 167°10′E), 675–680 m, 29 August 1985, one specimen 13 mm preserved length, leg. P. Bouchet, B. Métivier and B. Richer de Forges (MNHN). Île des Pins, New Caledonia, SMIB 8 Expedition, stn. DW193 (25°59′S, 168°21′E), 500–508 m, 1 February 1993, two specimens 10 mm preserved length, leg. P. Bouchet and B. Richer de Forges (MNHN).

External Morphology

The body is oval, almost rounded and somewhat elevated (Fig. 2B). The whole dorsum is covered with small, elongate tubercles. In general, tubercles are larger in the center of the dorsum. Some tubercles are clearly longer and are surrounded by areas with numerous short tubercles (Fig. 6D). The rhinophoral and branchial sheaths are edged by several long tubercles. The large, perfoliate rhinophores are composed of 38 lamellae. The gill consists of six short, bipinnate branchial leaves.

Ventrally, there are two short, conical oral tentacles (Fig. 7E). The anterior border of the

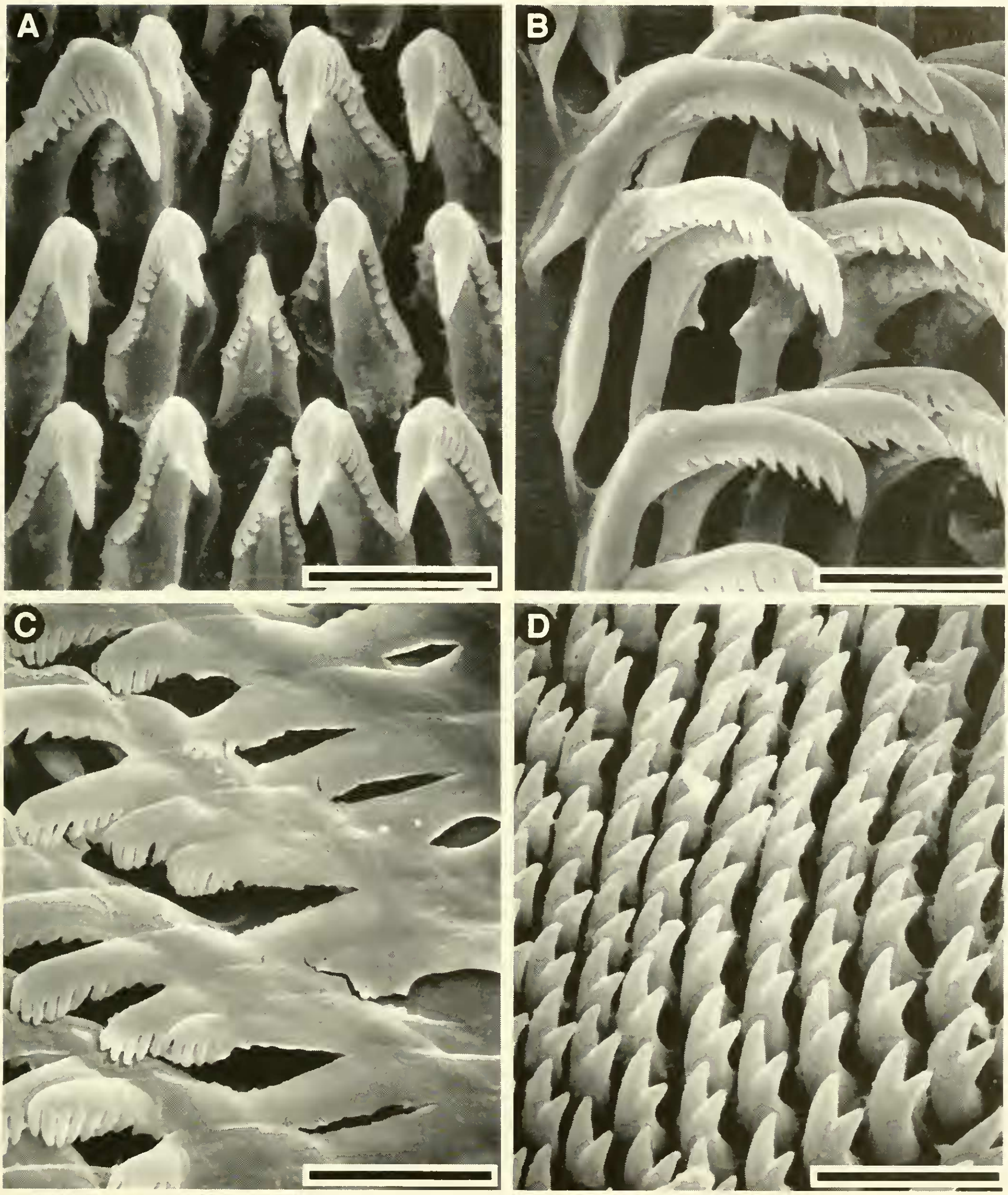

FIG. 5. *Cadlina* sp. specimen from Biocal (stn. DW14). A. Inner lateral teeth; scale bar = 15 μm. B. Mid-lateral teeth; scale bar = 15 μm. C. Outer lateral teeth; scale bar = 15 μm. D. Jaw elements; scale bar = 10 μm.

foot is grooved but not notched. The mantle margin is wider than the foot.

Based on the field notes, the color of the living animals is uniformly white, with yellowish tubercles. The rhinophores and gill are pale yellow.

Anatomy

The posterior end of the oral tube has six strong retractor muscles (Fig. 7C), which are attached to the body wall. The oval, muscular buccal bulb has two additional muscles. The

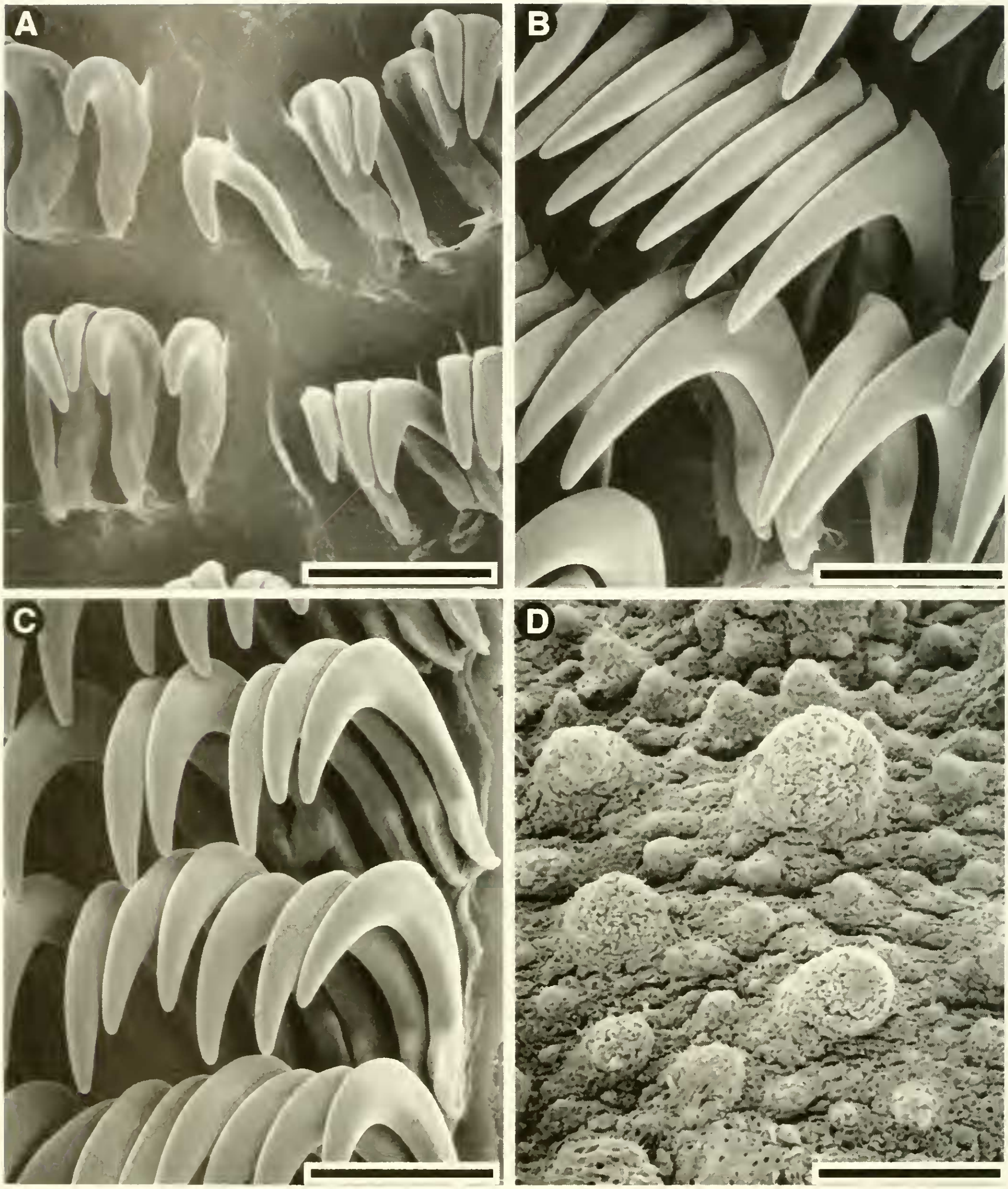

FIG. 6. *Austrodoris kerguelenensis,* specimen from SMIB 8 (stn. DW193). A. Inner lateral teeth; scale bar = 43 µm. B. Mid-lateral teeth; scale bar = 60 µm. C. Outer lateral teeth; scale bar = 60 µm. D. Dorsal tubercles; scale bar = 430 µm.

buccal bulb is as long as the oral tube. The labial armature is smooth. The radular formula is 36 × (56.0.56) in a 10 mm preserved length specimen. There are no rachidian teeth. The inner lateral teeth are hamate, having a single cusp, and they lack denticles (Fig. 6A). The teeth increase in size gradually towards the medial portion of the half-row (Fig. 6B). The outermost teeth are elongate and also lack denticles (Fig. 6C). The esophagus is long and connects to the stomach.

The ampulla is long and convoluted; it narrows into the gonoduct, which branches into the short oviduct and the prostate. The oviduct connects to the female glands near the center of the mass (Fig. 7B). The prostate

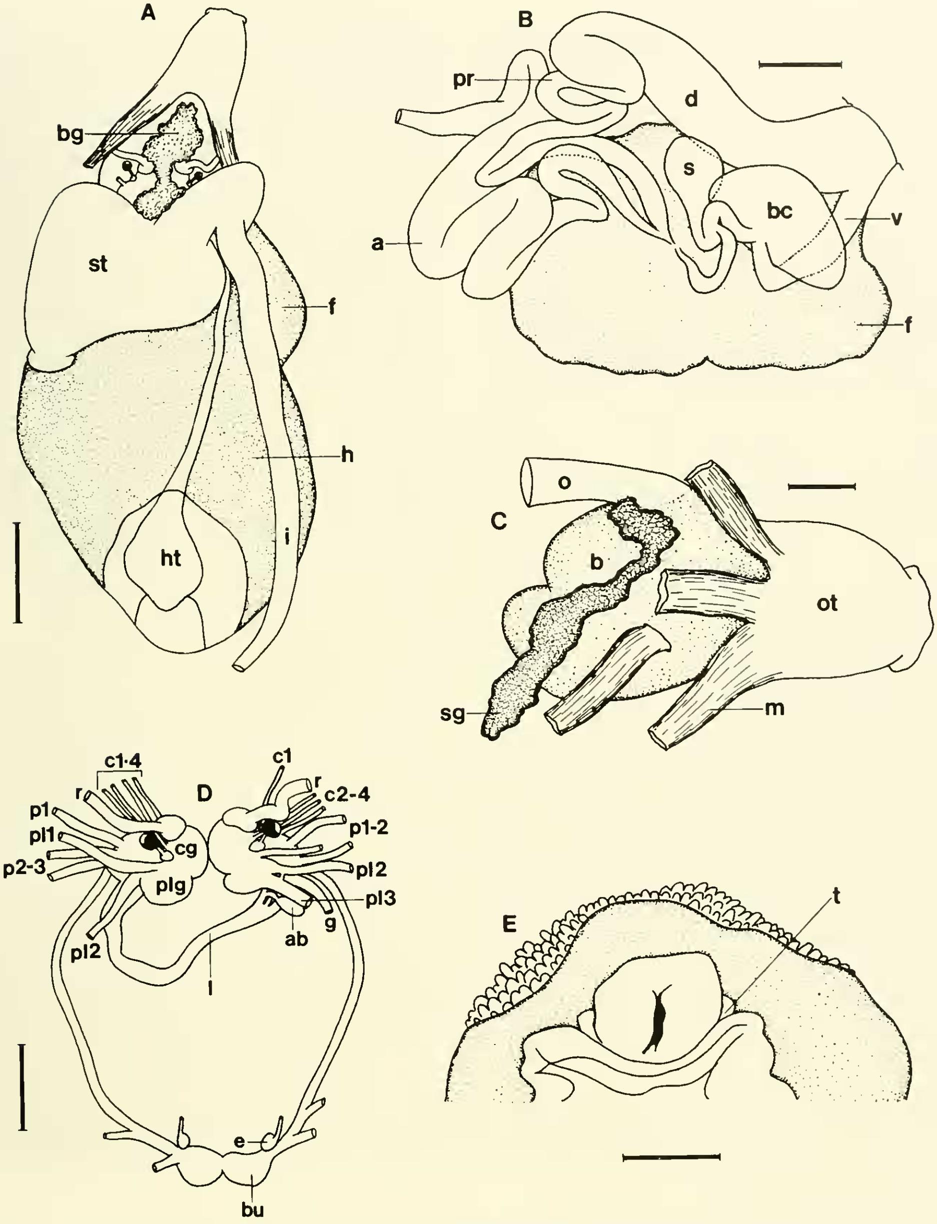

FIG. 7. *Austrodoris kerguelenensis,* specimen from SMIB 8 (stn. DW193). A. Dorsal view of the anatomy; scale bar = 1 mm. B. Reproductive system; scale bar = 0.5 mm. C. Anterior portion of the digestive system; scale bar = 0.5 mm. D. Central nervous system; scale bar = 0.5 mm. E. Mouth area; scale bar = 1 mm. Abbreviations: a, ampulla; ab, abdominal ganglion; b, buccal bulb; bc, bursa copulatrix; bg, blood gland; bu, buccal ganglion; c, cerebral nerve; cg, cerebral ganglion; d, deferent duct; e, esophageal ganglion; f, female glands; g, genital nerve; h, hermaphrodite and digestive glands; ht, heart; i, intestine; l, visceral loop; m, retractor muscle; o, esophagus; ot, oral tube; p, pedal nerve; pl, pleural nerve; plg, pleural ganglion; pr, prostate; r, rhinophoral nerve; s, seminal receptacle; sg, salivary gland; st, stomach; t, oral tentacle; v, vagina.

is tubular and convoluted; it expands again into the long and wide deferent duct. The deferent duct opens into a common atrium with the vagina. The penis is unarmed. The vagina is short and connects distally to the oval bursa copulatrix. From the bursa copulatrix leads another duct that branches into the uterine duct and the seminal receptacle. The seminal receptacle has a short, convoluted stalk. The bursa copulatrix is about three times larger than the seminal receptacle.

In the central nervous system (Fig. 7D), the cerebral and pleural ganglia are fused and distinct from the pedal ganglia. There are four cerebral nerves leading from each cerebral ganglion, three pleural nerves leading from the right pleural ganglion and three from the left ganglion. The buccal ganglia lie near the rest of the central nervous system, joined to the cerebral ganglia by two long nerves. Gastroesophageal, rhinophoral, and optical ganglia are present. The pedal ganglia are clearly separated, with three nerves leading from the left ganglion and two from the right ganglion. The pedal and parapedal commissures are enveloped together with the visceral loop along most of their length. There is an abdominal ganglion on the right side of the visceral loop.

The circulatory system (Fig. 7A) consists of a heart and two blood glands situated in front and behind the central nervous system.

Remarks

The external morphology and anatomy of the specimens from New Caledonia are very similar to the descriptions by Bergh (1884) and Wägele (1990) of *Austrodoris kerguelenensis,* and they clearly belong to the same species. In both the Antarctic and New Caledonia specimens, the dorsal tubercles are rounded, some of them being clearly longer, surrounded by areas with numerous short tubercles. Also, the reproductive system of the New Caledonia specimens has a very long, muscular deferent duct, a short tubular prostate, and a large, convoluted ampulla, identical to the description of Wägele (1990) for *A. kerguelenensis*. The proportions and arrangement of the bursa copulatrix and seminal receptacle is also very similar between the Antarctic and New Caledonia animals. Moreover, the radula of *A. kerguelenensis* is composed of numerous simple, hamate teeth (Wägele, 1990), very similar to those described here.

According to Wägele (1990), *Austrodoris kerguelenensis* is the only valid species of this genus. Recently, García et al. (1993), described *Austrodoris georgiensis* based on a single specimen collected from South Georgia in the Atlantic Antarctic sector. The only difference between *A. georgiensis* and *A. kerguelenensis* is the presence of an elongate bursa copulatrix in the former. Because other features of both nominal species (e.g., external morphology, radula, other reproductive organs), are identical, it is likely that the single specimen assigned to *A. georgiensis* is just an aberrant specimen of *A. kerguelenensis*. Another possibility is that the bursa copulatrix is more variable than assumed until now.

Austrodoris kerguelenensis, originally described from the Kerguelen Islands, is distributed throughout the Atlantic sector of the Antarctica (Wägele, 1990; García et al., 1993). Bouchet (1977) recorded *A. kerguelenensis* from Atlantic waters off Uruguay (as *Austrodoris macmurdensis*). The present record, from New Caledonia, is a considerable range extension for this species.

Austrodoris caeca Valdés, new species
(Figs. 2C, 8–10)

Material Examined

HOLOTYPE: Banc Combe, South Pacific, Musorstom 7 Expedition, stn. CP551 (12°15′S, 177°28′W), 791–795 m, 18 May 1992, 10 mm preserved length, leg. P. Bouchet, B. Métivier and B. Richer de Forges (MNHN).

PARATYPES: Banc Combe, South Pacific, Musorstom 7 Expedition, stn. CP552 (12°16′S, 177°28′W), 786–800 m, 18 May 1992, one specimen 12 mm preserved length, dissected, leg. P. Bouchet, B. Métivier and B. Richer de Forges (MNHN). Banc Tuscarora, South Pacific, Musorstom 7 Expedition, stn. CP562 (11°48′S, 178°22′W), 775–777 m, 19 May 1992, one specimen 12 mm preserved length, leg. P. Bouchet, B. Métivier and B. Richer de Forges (MNHN); stn. CP623 (12°34′S, 178°15′W), 1280–1300 m, 28 May 1992, one specimen 18 mm preserved length, dissected, leg. P. Bouchet, B. Métivier and B. Richer de Forges (MNHN). South of New Caledonia, Bathus 2 Expedition, stn. CP766 (22°10′S, 166°02′E), 650–724 m, 17 May 1993, one specimen 12 mm preserved length, leg. P. Bouchet and B. Richer de Forges (CASIZ 121096). Norfolk Ridge, New Caledo-

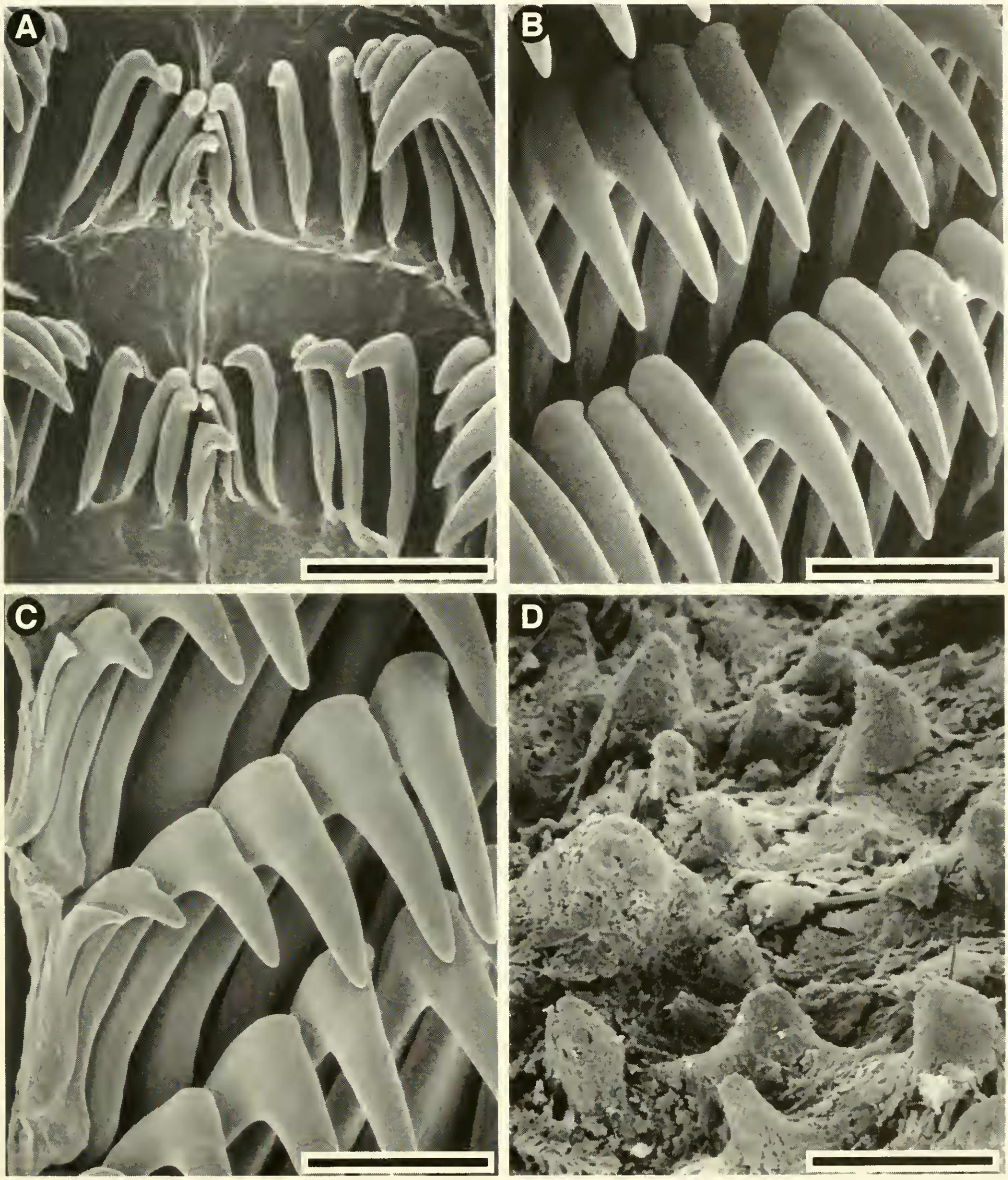

FIG. 8. *Austrodoris caeca,* new species, paratype from Musorstom 7 (stn. CP552). A. Inner lateral teeth; scale bar = 60 μm. B. Mid-lateral teeth; scale bar = 75 μm. C. Outer lateral teeth; scale bar = 75 μm. D. Dorsal tubercles; scale bar = 200 μm.

nia, Bathus 3 Expedition, stn. CC848 (23°02′S, 166°53′E), 680–700 m, 1 December 1993, two specimens 14 mm preserved length, leg. P. Bouchet, B. Richer de Forges and A. Warén (MNHN). New Caledonia, Halipro 1 Expedition, stn. CH876 (23°10′S, 166°49′E), 870–1000 m, 31 March 1994, 23 mm preserved length, dissected, leg. B. Richer de Forges (MNHN). Vanuatu, South Pacific, Musorstom 8 Expedition, stn. CP1074 (15°48′S, 167°24′E), 775–798 m, 4 October 1994, one specimen 13 mm preserved length, dissected, leg. P. Bouchet and B. Richer de Forges (MNHN).

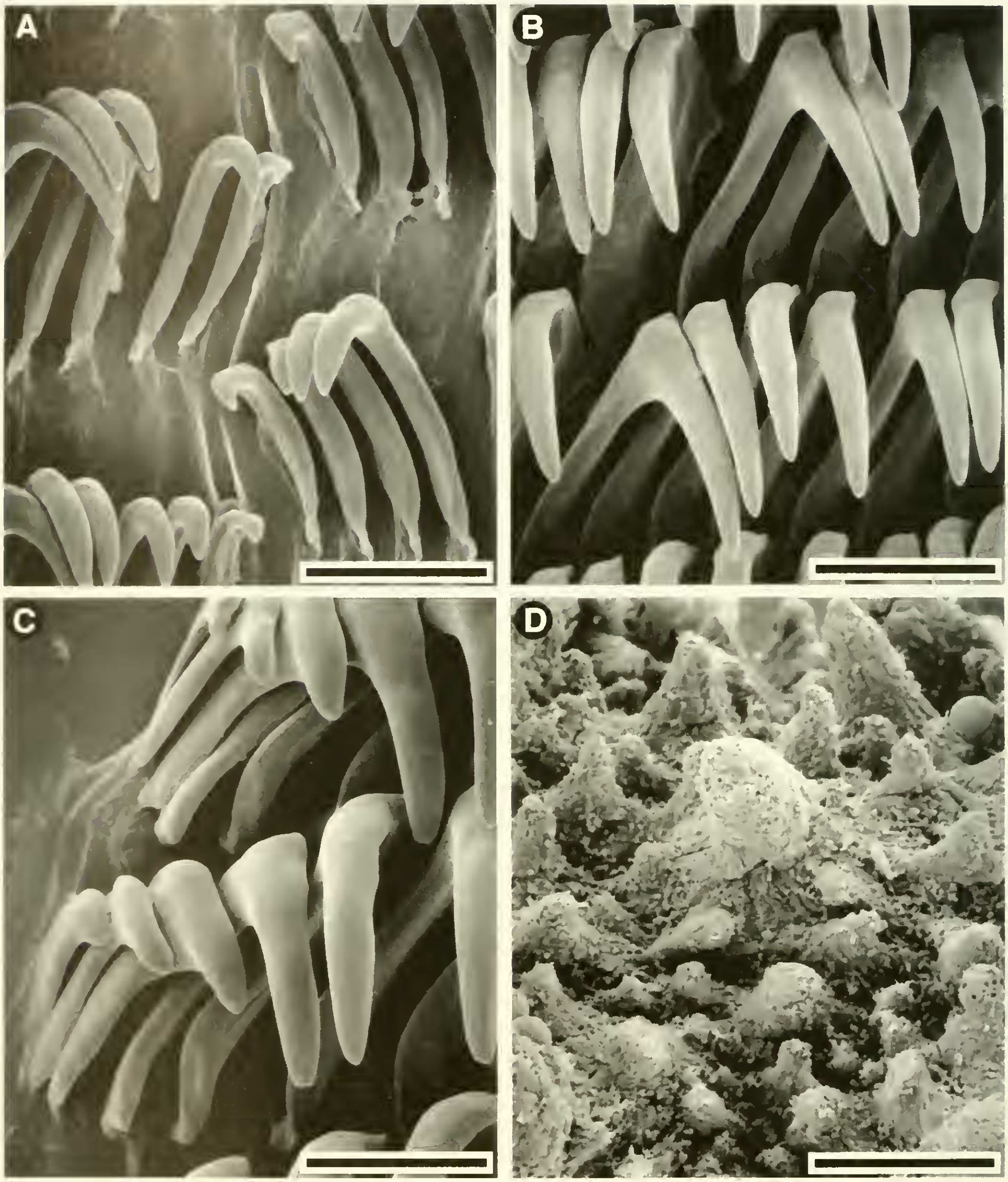

FIG. 9. *Austrodoris caeca*, new species, paratype from Musorstom 8 (stn. CP1074). A. Inner lateral teeth; scale bar = 60 μm. B. Mid-lateral teeth; scale bar = 100 μm. C. Outer lateral teeth; scale bar = 75 μm. D. Dorsal tubercles; scale bar = 250 μm.

External Morphology

The body is oval, almost rounded and somewhat elevated (Fig. 2C). The whole dorsum is covered with small, rounded tubercles. Some of them are irregularly distributed and larger than the others (Figs. 8D, 9D). The rhinophoral sheaths are elevated and covered with small tubercles. The large, perfoliate rhinophores are composed of 41 lamellae. The gill consists of six short, bipinnate branchial leaves.

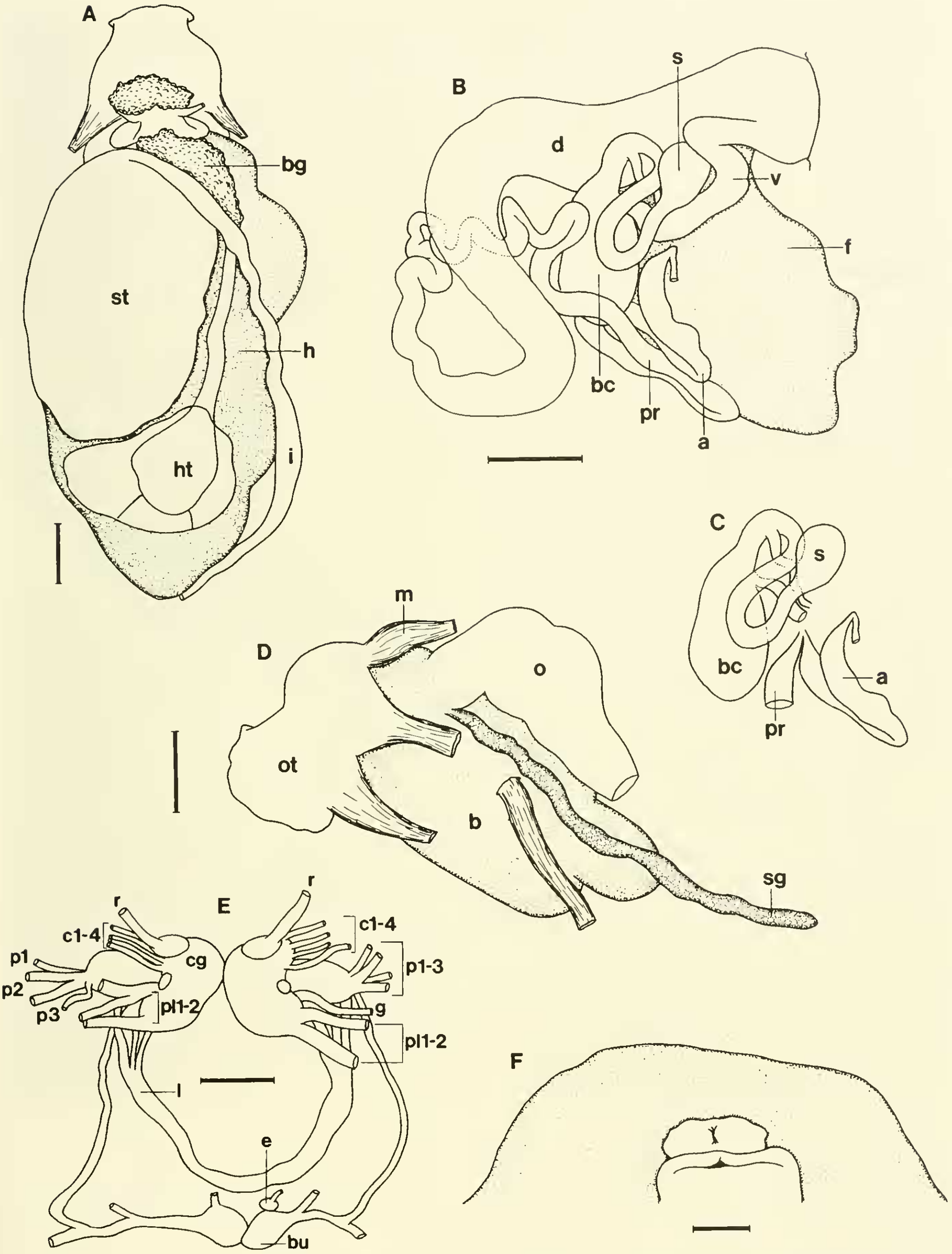

FIG. 10. *Austrodoris caeca,* new species, paratype from Musorstom 7 (stn. CP552). A. Dorsal view of the anatomy, scale bar = 1 mm. B. Reproductive system; scale bar = 1 mm. C. Detail of several reproductive organs; scale bar = 1 mm. D. Anterior portion of the digestive system; scale bar = 1 mm. E, Central nervous system; scale bar = 0.5 mm. F, Mouth area; scale bar = 1 mm. Abbreviations: a, ampulla; b, buccal bulb; bc, bursa copulatrix; bg, blood gland; bu, buccal ganglion; c, cerebral nerve; cg, cerebral ganglion; d, deferent duct; e, esophageal ganglion; f, female glands; g, genital nerve; h, hermaphrodite and digestive glands; ht, heart; i, intestine; l, visceral loop; m, retractor muscle; o, esophagus; ot, oral tube; p, pedal nerve; pl, pleural nerve; pr, prostate; r, rhinophoral nerve; s, seminal receptacle; sg, salivary gland; st, stomach; v, vagina.

Ventrally, there are no oral tentacles (Fig. 10F). The anterior border of the foot is grooved but not notched.

The color of the living animals is unknown. The preserved specimens are uniformly cream or pinkish. The rhinophores and gill are pale cream.

Anatomy

The posterior end of the oral tube has six strong retractor muscles (Fig. 10D), which are attached to the body wall. The oval, muscular buccal bulb has two additional muscles. The buccal bulb is three times longer than the oral tube. The labial armature is smooth. The radular formula is 21 × (30.0.30) in a 12 mm preserved length specimen and 26 × (36.0.36) in a 13 mm preserved length specimen. There are no rachidian teeth. The inner lateral teeth are hamate, having a single cusp, and they lack denticles (Figs. 8A, 9A). The teeth increase in size gradually towards the medial portion of the half-row (Figs. 8B, 9B). The outermost teeth are elongate but shorter than the adjacent ones, and also lack denticles (Figs. 8C, 9C). The esophagus is long and connects directly to the stomach.

The ampulla is thin and elongate; it narrows into the gonoduct, which branches into the short oviduct and the prostate (Fig. 10C). The oviduct connects to the female glands near the center of the mass. The prostate is tubular and elongate (Fig. 10B); it narrows slightly and expands into the long, wide and strongly muscular deferent duct. The deferent duct opens into a common atrium with the vagina. The penis is unarmed and very long, about 2/3 of the ejaculatory portion of the deferent duct length. The vagina is elongate. At its proximal end, the vagina connects to the oval bursa copulatrix. From the bursa copulatrix leads another duct that connects to the seminal receptacle and the uterine duct. The seminal receptacle has a long, convoluted stalk. The bursa copulatrix is about eight times larger than the seminal receptacle.

In the central nervous system (Fig. 10E), the cerebral and pleural ganglia are fused and distinct from the pedal ganglia. There are four cerebral nerves leading from each cerebral ganglion, and two pleural nerves lead from each pleural ganglion. The buccal ganglia lie near the rest of the central nervous system, joined to the cerebral ganglia by two long nerves. Gastroesophageal, rhinophoral, and optical ganglia are present. There are no eyes. The pedal ganglia are clearly separated, with three nerves leading from each. The pedal and parapedal commissures are enveloped together with the visceral loop along most of their length.

The circulatory system (Fig. 10A) consists of a heart and two blood glands situated in front and behind the central nervous system.

Etymology

From the Latin *caecum* (blind), in reference to the lack of eyes in this species.

Remarks

The genus *Austrodoris* is very closely related to *Archidoris* Bergh, 1878. According to Wägele (1990), the main differences between these two genera are that in *Austrodoris* most of the length of the deferent duct is encased within a muscular sheath, there is no glans penis, and the seminal receptacle and bursa copulatrix insert opposite and not serially. The genus *Austrodoris* appears to be restricted to the Southern Hemisphere, whereas *Archidoris* is mainly distributed in the Northern Hemisphere. An anatomical study and comparison between the type species of both genera is necessary before their systematic status can be determined. In the meanwhile, I follow Wägele's (1990) criteria and maintain *Austrodoris* as a valid genus.

Austrodoris caeca clearly belongs to the genus *Austrodoris* in lacking a glans penis, having a very large, elongate and strongly muscular deferent duct, longer than the prostate, smooth and hamate radular teeth, and a smooth labial cuticle.

Anatomically, *A. caeca* differs from *Austrodoris kerguelenensis* in having a seminal receptacle with a long stalk, having a much shorter ampulla, and in lacking eyes. In addition, the outermost lateral teeth of *A. caeca* are very short compared to the mid-laterals, whereas in *A. kerguelenensis* they are proportionally larger.

Austrodoris laboutei Valdés, new species

(Figs. 2F, 11, 12)

Material Examined

HOLOTYPE: East of New Caledonia, Bathus 1 Expedition, stn. CP711 (21°43′S, 166°36′E), 315–327 m, 19 March 1993, one specimen 15 mm preserved length, dis-

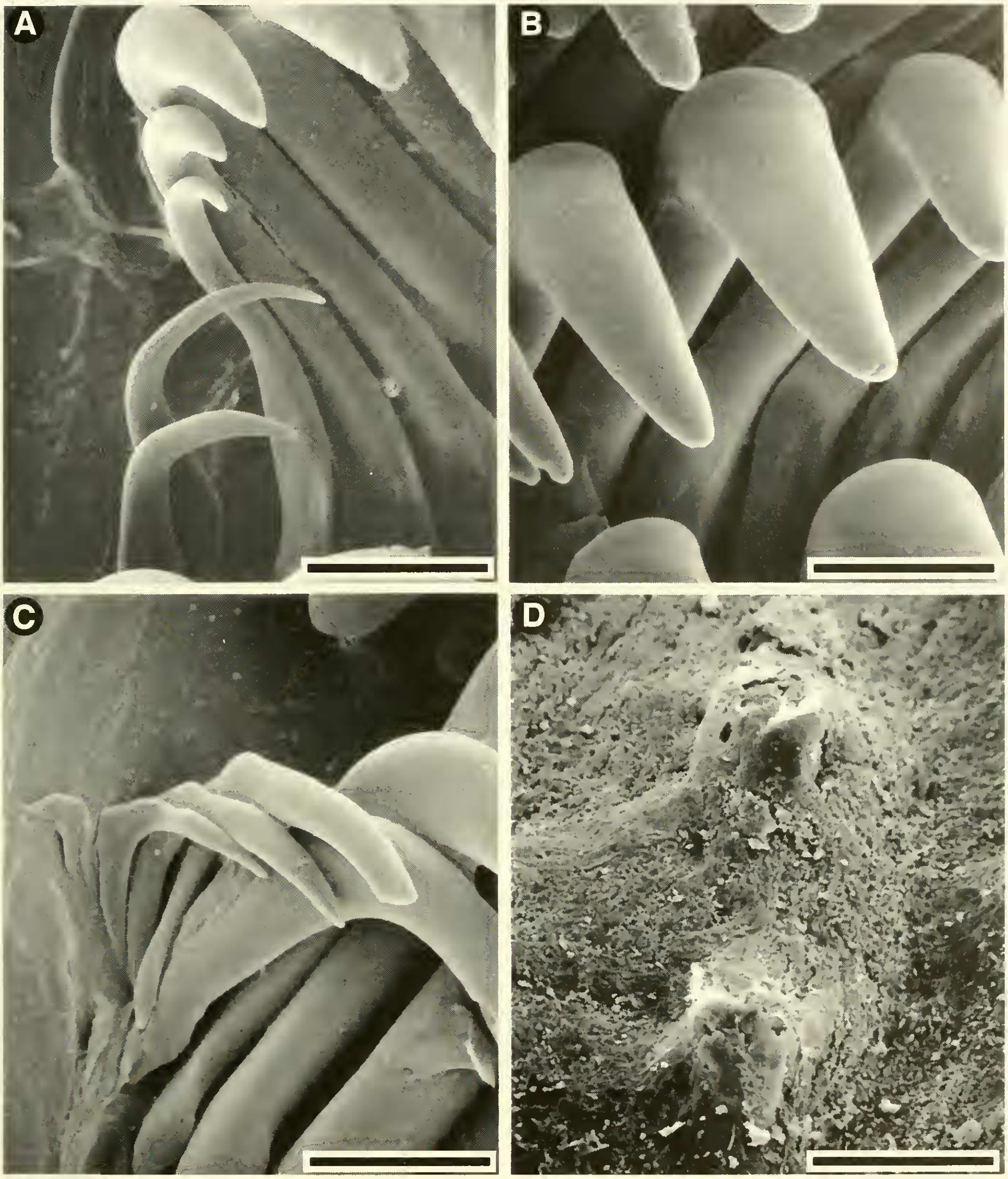

FIG. 11. *Austrodoris laboutei,* new species, holotype. A. Inner lateral teeth; scale bar = 43 µm. B. Mid-lateral teeth; scale bar = 75 µm. C, Outer lateral teeth; scale bar = 43 µm. D, Dorsal tubercles; scale bar = 75 µm.

sected, leg. P. Bouchet and B. Richer de Forges (MNHN).

External Morphology

The body is elongate and high (Fig. 2F). The mantle margin is very reduced. The whole dorsum is covered with small, rounded tubercles, all of them similar in size (Fig. 11D). The rhinophoral sheaths are low, situated very anteriorly, and covered with small tubercles. The large, perfoliate rhinophores are composed of 19 lamellae. The gill sheath has a wide opening and it is situated very posteriorly. The gill consists of seven long, tripinnate branchial leaves.

Ventrally, the oral tentacles are wide, short, and grooved (Fig. 12E). The anterior border of

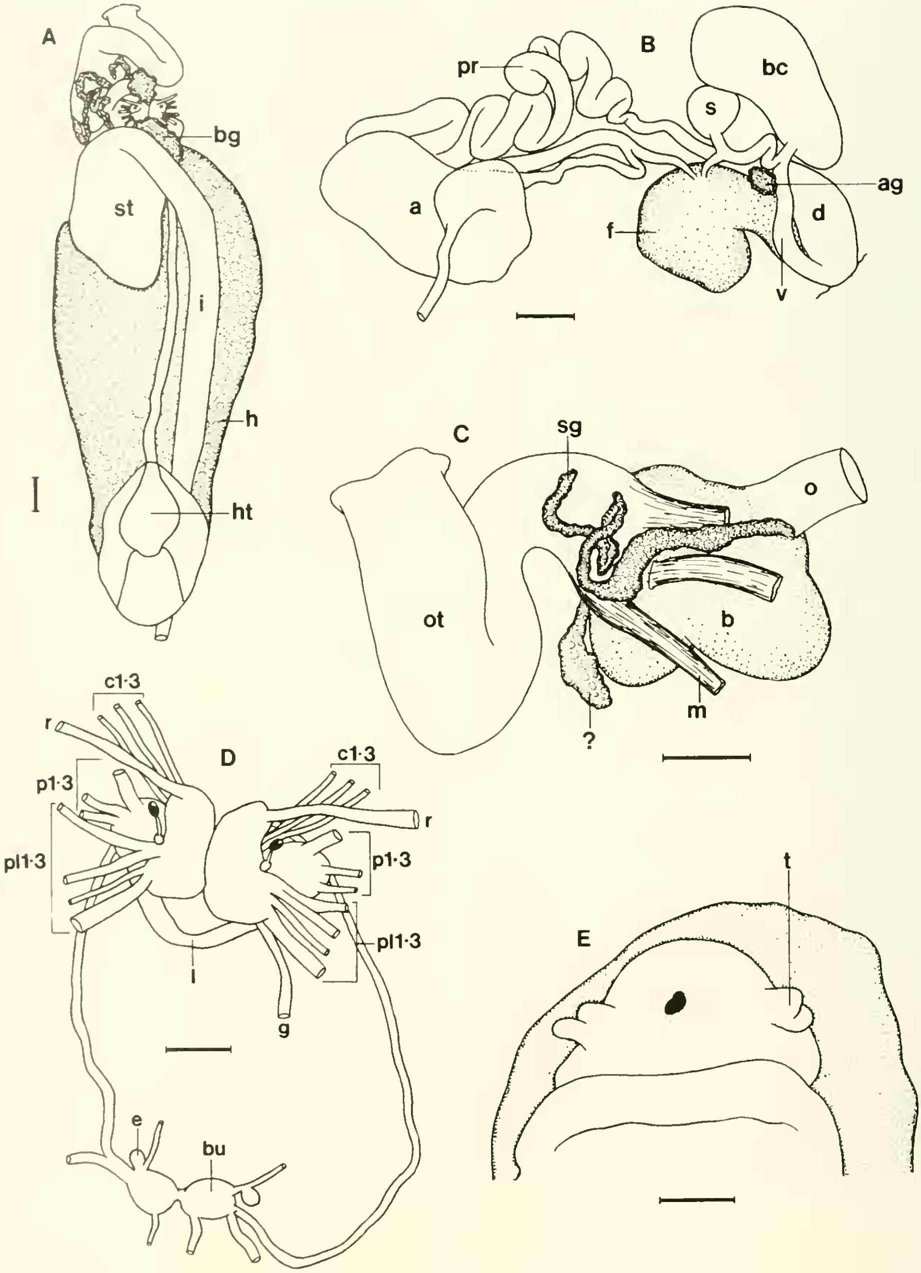

FIG. 12. *Austrodoris laboutei* new species, holotype. A. Dorsal view of the anatomy; scale bar = 1 mm. B. Reproductive system; scale bar = 0.5 mm. C. Anterior portion of the digestive system; scale bar = 1 mm. D. Central nervous system; scale bar = 0.5 mm. E. Mouth area; scale bar = 1 mm. Abbreviations: a, ampulla; ag, accessory gland; b, buccal bulb; bc, bursa copulatrix; bg, blood gland; bu, buccal ganglion; c, cerebral nerve; d, deferent duct; e, esophageal ganglion; f, female glands; g, genital nerve; h, hermaphrodite and digestive glands; ht, heart; i, intestine; l, visceral loop; m, retractor muscle; o, esophagus; ot, oral tube; p, pedal nerve; pl, pleural nerve; pr, prostate; r, rhinophoral nerve; s, seminal receptacle; sg, salivary gland; st, stomach; t, oral tentacle; v, vagina.

the foot is grooved but not notched. The foot is wide.

Based on the field notes, the color of the living animals is cream grayish. The dorsum is covered with a number of small, brown spots. The rhinophores are pale brown, and the gill is cream grayish with brown spots. The preserved specimen is uniformly cream.

Anatomy

The posterior end of the oral tube has four strong retractor muscles (Fig. 12C), which are attached to the body wall. The oval, muscular buccal bulb has two additional muscles. Two long salivary glands are attached to the buccal bulb at the point where the esophagus connects. There is another glandular structure that connects ventrally to the buccal bulb at the point where the oral tube opens into the buccal bulb. The buccal bulb is one-third the length of the oral tube. The labial armature is smooth. The radular formula is 15 × (16.0.16) in a 16 mm preserved length specimen. There are no rachidian teeth. The inner lateral teeth are hamate, having a very long, thin cusp that lacks denticles (Fig. 11A). The teeth increase in size suddenly towards the medial portion of the half-row. The mid-lateral teeth are long, having a short, conical cusp, and they lack denticles (Fig. 11B). The outermost teeth are small and also lack denticles (Fig. 11C). The esophagus is long and connects directly to the stomach.

The ampulla is wide and convoluted; it narrows into the gonoduct, which branches into the long oviduct and the prostate (Fig. 12B). The oviduct connects to the female glands near the center of the mass. The prostate is tubular and elongate; it narrows slightly and expands again into the wide deferent duct. The deferent duct opens into a common atrium with the vagina. The penis occupies the whole ejaculatory portion of the deferent duct. The vagina is short. At its proximal end, the vagina connects to the irregular bursa copulatrix and to another short, wide duct that connects to the seminal receptacle and the uterine duct. The seminal receptacle has a short stalk. The bursa copulatrix is about eight times larger than the seminal receptacle.

In the central nervous system (Fig. 12D), the cerebral and pleural ganglia are fused and distinct from the pedal ganglia. There are three cerebral nerves leading from each cerebral ganglion, and three pleural nerves lead from each pleural ganglion. The buccal ganglia lie near the rest of the central nervous system, joined to the cerebral ganglia by two long nerves. Gastroesophageal, rhinophoral, and optical ganglia are present. The pedal ganglia are clearly separated, with three nerves leading from each. The pedal and parapedal commissures are enveloped together with the visceral loop.

The circulatory system (Fig. 12A) consists of a heart and two blood glands situated in front and behind the central nervous system.

Etymology

After Pierre Laboute, who photographed specimens studied in this paper.

Remarks

Austrodoris laboutei belongs to the genus *Austrodoris* in lacking a glans penis, having a strongly muscular deferent duct, smooth and hamate radular teeth, and a smooth labial cuticle. Other features of this species that are also present in members of the genus *Austrodoris* are short, non-digitiform oral tentacles and simple dorsal tubercles. However, the deferent duct of *A. laboutei* is much shorter than in other species of the genus, and there is a gland that connects the oral tube and the buccal bulb and an accessory gland in the reproductive system, both of which are absent in other members of the genus. The allocation of *A. laboutei* in the genus *Austrodoris* is thus provisional, until a phylogenetic analysis of other related species will allow a more precise definition of the diagnostic characters of the genera *Archidoris* and *Austrodoris.*

Austrodoris laboutei is clearly distinguishable from other species of the genus by the body shape, with a very reduced mantle margin. The coloration of this species, cream grayish with small brown spots is different from that of *A. kerguelenensis,* which is uniformly white with yellowish tubercles.

Anatomically, *A. laboutei* differs from *Austrodoris kerguelenensis* and *A. caeca* in having an accessory gland in the reproductive system, a much longer prostate, and a very large and irregular bursa copulatrix. In addition, the innermost and outermost radular teeth of *A. laboutei* are very long and thin compared to those of other species of the genus. On the contrary, the mid-laterals of *A. laboutei* are stronger than those of *A. kerguelenensis* and *A. caeca.*

Genus ***Goslineria*** Valdés, new genus

Type Species: *Goslineria callosa* Valdés, new species, here designated.

Diagnosis

Body elevated, oval, stiffened by numerous integumentary spicules. Dorsum covered with simple, conical tubercles. Anterior border of the foot grooved, not notched. Labial cuticle unarmed. Radula without rachidian teeth. Inner and mid-lateral teeth simple, hamate. Outermost lateral teeth with numerous, small denticles. Prostate flattened, flattened. Penis unarmed. Genital atrium with several large sacs, each containing a long, simple, flexible spine.

Etymology

Dedicated to Terry Gosliner, who made invaluable comments on the manuscript and provided financial support for this study.

Remarks

The presence of several sacs in the reproductive system, each containing a flexible copulatory spine, is the most distinctive feature of this new genus. Species of *Paradoris* may also have sacs with copulatory spines associated with the atrium, but in this genus the spines are rigid. Besides, species of *Paradoris* have jaws, armed with numerous denticles, whereas in *Goslineria* the labial cuticle is smooth. The new genus *Pharodoris* has two large, rigid copulatory spines. However, *Pharodoris* is different from *Goslineria* in having bifid spines, a highly elevated branchial sheath, and a tubular prostate. Other genera with copulatory spines are *Hoplodoris, Asteronotus, Jorunna,* and *Sclerodoris,* but in all those the spines are rigid and situated in the accessory gland, not in separate sacs (Gosliner & Behrens, 1998; Valdés & Gosliner, in press). Moreover, *Jorunna* and *Sclerodoris* have caryophyllidia, which are absent in *Goslineria, Asteronotus, Pharodoris* and *Paradoris.*

Goslineria callosa Valdés, new species
(Figs 13A, 14, 15, 16B)

Material Examined

HOLOTYPE: Philippines, Musorstom 2 Expedition, stn. CP41 (13°16′N, 122°46′E), 166–172 m, 25 November 1980, 21 mm preserved length, leg. P. Bouchet (MNHN).

External Morphology

The body is elevated and oval (Fig. 13A). The dorsum is covered with simple, conical tubercles (Fig. 14D). Some tubercles are clearly larger than the others. The perfoliate rhinophores are each composed of 22 lamellae. There are seven tripinnate branchial leaves. The rhinophoral and branchial sheaths are somewhat elevated, bearing numerous tubercles. Ventrally, there are no oral tentacles (Fig. 15F). The anterior border of the foot is grooved, not notched. The mantle margin is as wide as the foot.

Based on the photographs, the color of the living animal is uniformly pale cream. The rhinophores and gill have the same color as the dorsum.

Anatomy

The posterior end of the oral tube has six strong retractor muscles (Fig. 15E), which are attached to the body wall. The oval, muscular buccal bulb has two additional muscles. The buccal bulb tube is about twice as long as the oral tube. The labial cuticle is smooth. The radular formula is 39 × (42.0.42) in a 21 mm preserved length specimen. There are no rachidian teeth. The inner and mid-lateral teeth are hamate, having a single cusp, and they lack denticles (Fig. 14A). The teeth increase in size gradually towards the medial portion of the half-row (Fig. 14B). The outermost lateral teeth are also hamate and have numerous, small denticles (Fig. 14C). The esophagus is very long, convoluted, and connects directly to the stomach (Fig. 15A).

The ampulla is long and convoluted; it narrows into the gonoduct, which branches into a short oviduct and the prostate (Fig. 15C). The oviduct enters the female glands near the nidamental opening. The prostate is large and flattened (Fig 15B); it narrows and expands again into the long, wide and muscular deferent duct. The deferent duct opens into a common atrium with the vagina. The atrium has six long sacs, each one containing a long, flexible copulatory spine (Figs. 15B, 16B). The largest copulatory spine reaches up to 1.5 mm in length. The penis is unarmed. The vagina is very wide. At its proximal end, the

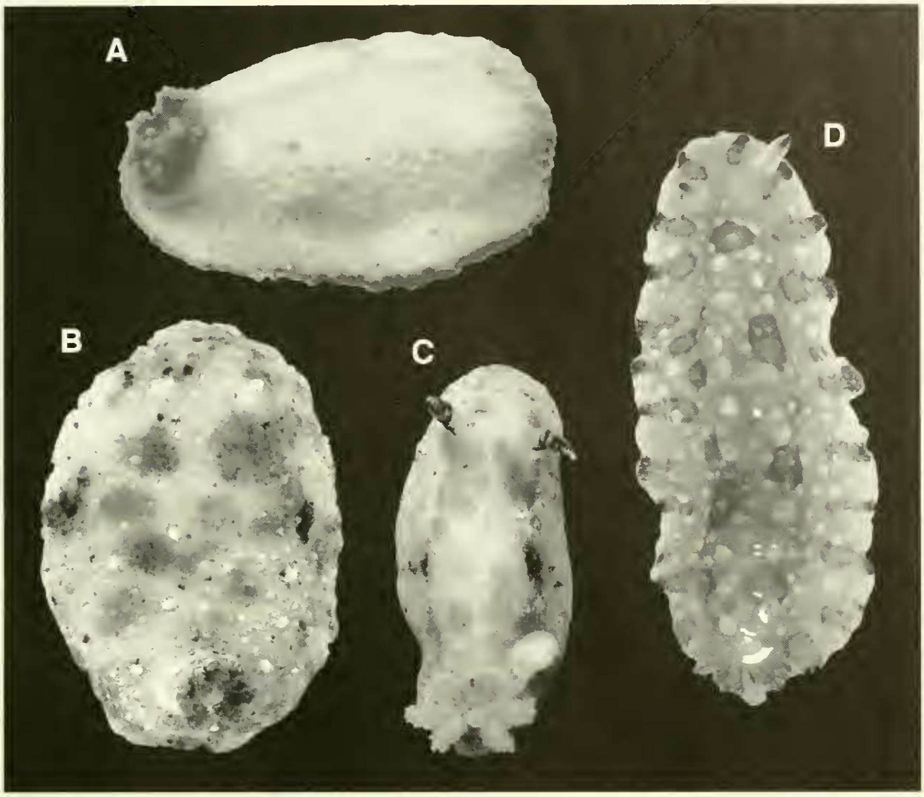

FIG. 13. Living animals. A. *Goslineria callosa*, new genus and species, holotype. B. *Paradoris araneosa*, new species, paratype from SMIB 8 (stn. DW182–184), photo J. L. Menou. C. *Paradoris imperfecta*, new species, holotype, photo P. Laboute. D. *Dendrodoris brodieae*, new species, paratype from Chalcal 2 (stn. DW81), photo P. Laboute.

vagina connects to the large and oval bursa copulatrix. From the vagina leads another very short duct that connects to the seminal receptacle and the long uterine duct. The bursa copulatrix is about five times larger than the seminal receptacle.

In the central nervous system (Fig. 15D), the cerebral and pleural ganglia are fused and distinct from the pedal ganglia. There are three cerebral nerves leading from each cerebral ganglia, and two pleural nerves lead from each pleural ganglion. The buccal ganglia lie near the rest of the central nervous system, joined to the cerebral ganglia by two long nerves. Gastroesophageal, rhinophoral, and optical ganglia are present. The pedal ganglia are clearly separated, with four (right) or three (left) nerves leading from them. The pedal and parapedal commissures are enveloped together with the visceral loop along all their length.

The circulatory system (Fig. 15A) consists of a heart and a blood gland situated over the central nervous system.

Etymology

From the Latin *callosus* (hard skin), in reference to the hard texture of the mantle of this species.

Remarks

This species is clearly distinguishable from other dorids previously described by the presence of several, flexible copulatory spines in the reproductive system.

Genus ***Pharodoris*** Valdés, new genus

Type Species: *Pharodoris diaphora* Valdés, new species, here designated.

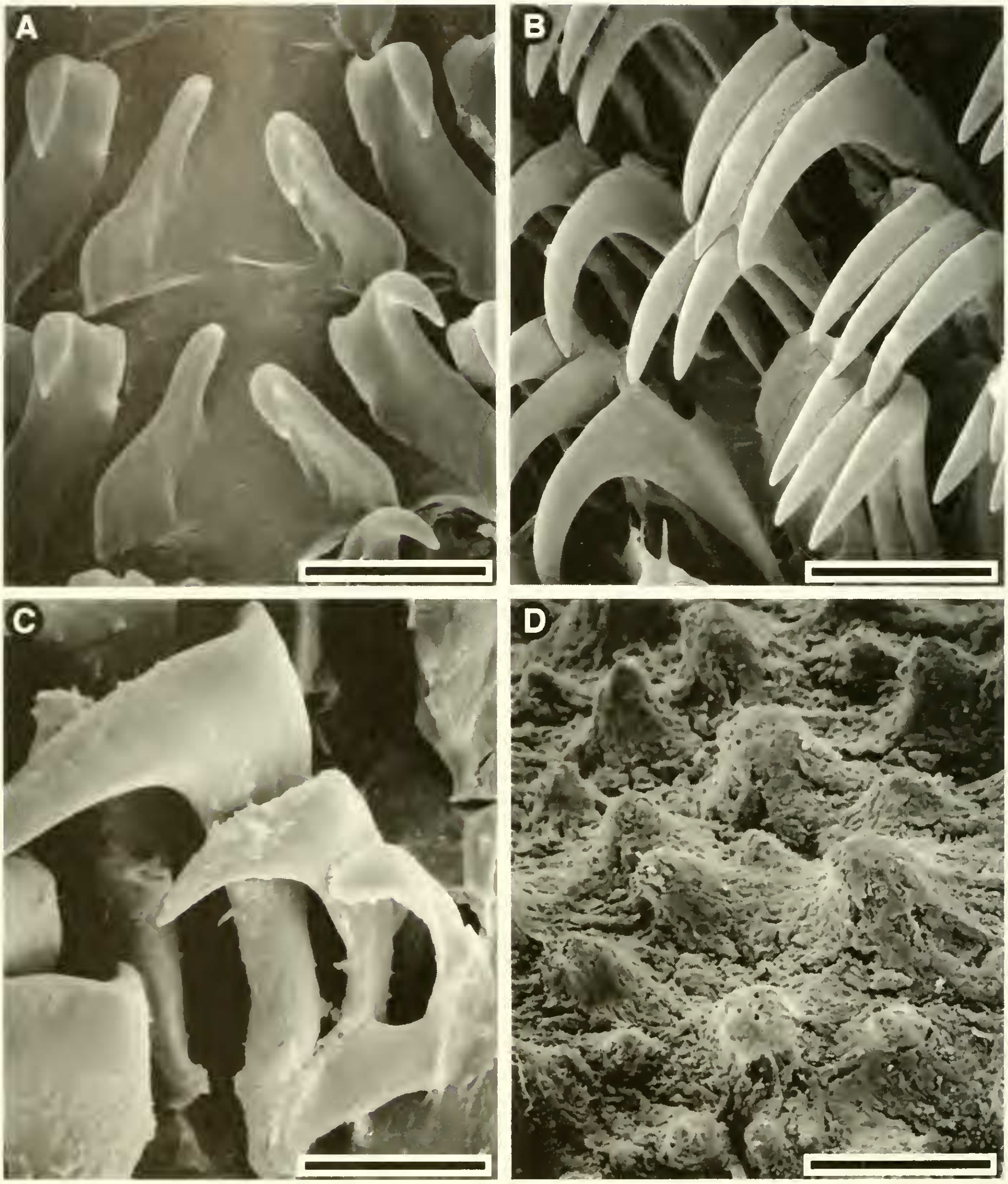

FIG. 14. *Goslineria callosa,* new genus and species, holotype. A. Inner lateral teeth; scale bar = 43 µm. B. Mid-lateral teeth; scale bar = 75 µm. C. Outer lateral teeth; scale bar = 43 µm. D. Dorsal tubercles; scale bar = 250 µm.

Diagnosis

Body elevated, oval, stiffened by numerous integumentary spicules. Dorsum covered with simple, conical tubercles. Branchial sheath very elevated. Anterior border of the foot grooved, not notched. Oral tentacles short. Labial cuticle unarmed. Radula without rachidian teeth. Inner and mid-lateral teeth simple, hamate. Outermost lateral teeth with numerous, small denticles. Prostate long, tubular. Penis unarmed. Genital atrium with

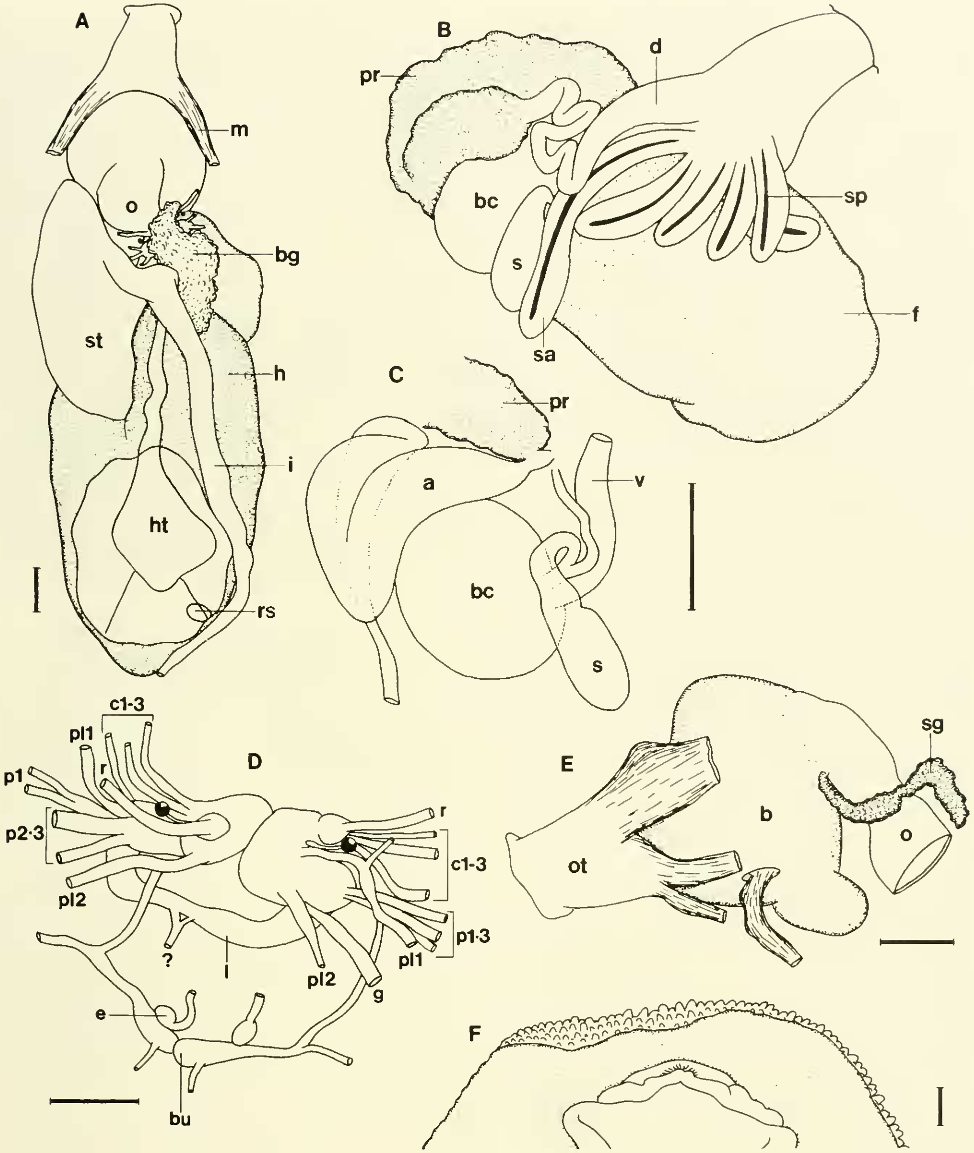

FIG. 15. *Goslineria callosa,* new genus and species, holotype. A. Dorsal view of the anatomy; scale bar = 1 mm. B. Reproductive system; scale bar = 1 mm. C. Detail of several reproductive organs; scale bar = 1 mm. D. Central nervous system; scale bar = 0.5 mm. E. Anterior portion of the digestive system; scale bar = 1 mm. F, Mouth area; scale bar = 1 mm. Abbreviations: a, ampulla; b, buccal bulb; bc, bursa copulatrix; bg, blood gland; bu, buccal ganglion; c, cerebral nerve; d, deferent duct; e, esophageal ganglion; f, female glands; g, genital nerve; h, hermaphrodite and digestive glands; ht, heart; i, intestine; l, visceral loop; m, retractor muscle; o, esophagus; ot, oral tube; p, pedal nerve; pl, pleural nerve; pr, prostate; r, rhinophoral nerve; rs, renal syrinx; s, seminal receptacle; sa, copulatory spine sac; sg, salivary gland; sp, copulatory spine; st, stomach; v, vagina.

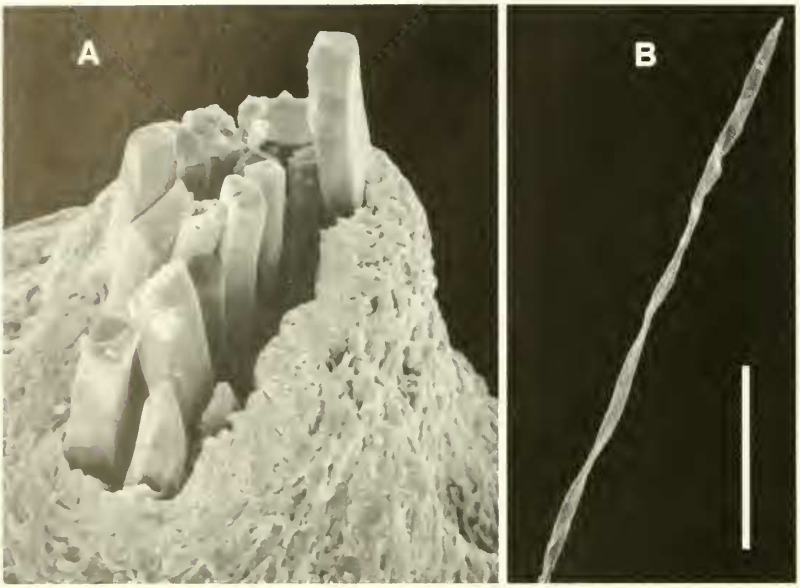

FIG. 16. Copulatory organs. A. Solid structures in the accessory gland of *Geitodoris pallida*, new species, holotype. B. Copulatory spine of *Goslineria callosa*, new genus and species, holotype.

two large glands, each containing a long, bifid, rigid spine.

Etymology

From the Ancient Greek *pharos* (lighthouse), in reference to the shape of the branchial sheath, that resembles a lighthouse tower.

Remarks

The new genus *Pharodoris* is clearly distinguishable from other genera of cryptobranch dorids previously described. It has several unique features, such as a very elevated branchial sheath and the presence of two large glands in the atrium, armed with bifid, rigid copulatory spines.

The presence of simple dorsal tubercles, a radula lacking rachidian teeth and having simple, hamate lateral teeth (except the outermost), absence of labial armature, presence of a tubular prostate, and the anterior border of the foot grooved but not notched, relate *Pharodoris* with *Archidoris* and *Austrodoris*. However, these two genera lack accessory glands with copulatory spines, and the branchial sheath is not so elevated (Wägele, 1990; Valdés & Gosliner, in press).

Pharodoris diaphora Valdés, new species
(Figs 2D, 17, 18, 19C)

Material Examined

HOLOTYPE: East of New Caledonia, Bathus 1 Expedition, stn. CP707 (21°43′S, 166°36′E), 347–375 m, 19 March 1993, 19 mm preserved length, leg. P. Bouchet and B. Richer de Forges (MNHN).

PARATYPES: New Caledonia, Musorstom 4 Expedition, stn. DW231 (22°34′S, 167°10′E), 75 m, 1 October 1985, one specimen 7 mm preserved length, leg. P. Bouchet and B. Richer de Forges (MNHN). East of New Caledonia, Bathus 1 Expedition, stn. CP710 (21°43′S, 166°36′E), 320–386 m, 19 March 1993, one specimen 18 mm preserved length, leg. P. Bouchet and B. Richer de Forges (CASIZ 121097); stn. CP711 (21°43′S, 166°36′E), 315–327 m, 19 March 1993, one specimen 16 mm preserved length, dissected, leg. P. Bouchet and B. Richer de Forges (MNHN). Vanuatu, Musorstom 8 Expedition, stn. DW964 (20°20′S, 169°49′E), 360–408 m, 21 September 1994, one speci-

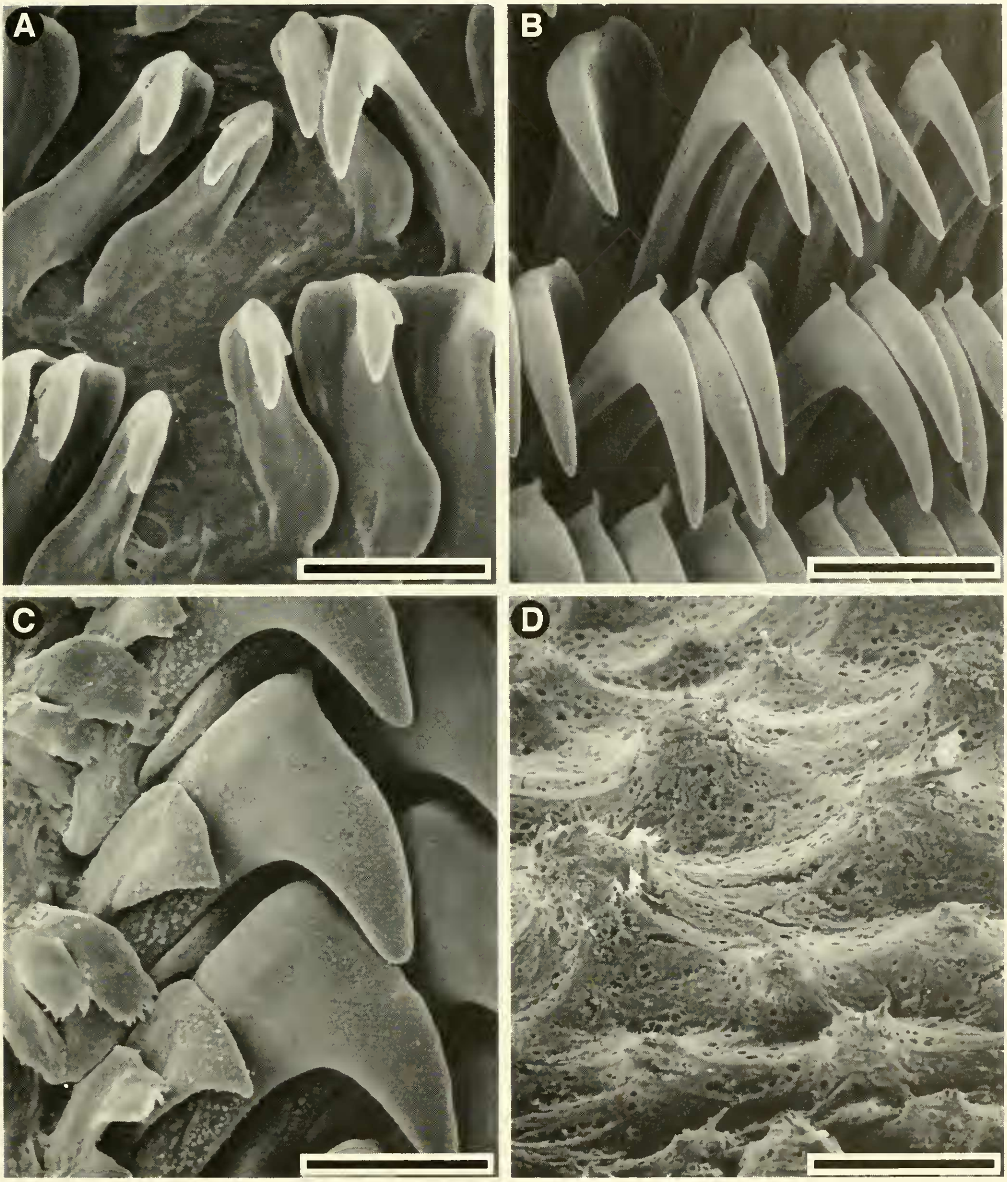

FIG. 17. *Pharodoris diaphora*, new genus and species, paratype from Bathus 1 (stn. CP711). A. Inner lateral teeth; scale bar = 43 μm. B. Mid-lateral teeth; scale bar = 75 μm. C. Outer lateral teeth; scale bar = 60 μm. D. Dorsal tubercles; scale bar = 300 μm.

men 9 mm preserved length, leg. P. Bouchet and B. Richer de Forges (MNHN).

ADDITIONAL MATERIAL: Passe Deverd, outer Barrier Reef, near Koumac, New Caledonia (20°45.2′S, 164°15.2′E), 53 m, 22 October 1993, 3 specimens 10–12 mm long alive, leg. W. Rudman (AM C200596).

External Morphology

The body is somewhat elevated, oval (Fig. 2D). The dorsum is covered with simple, conical tubercles. Some of them, more abundant in the center of the body are twice as large as the others. There are several spicules pro-

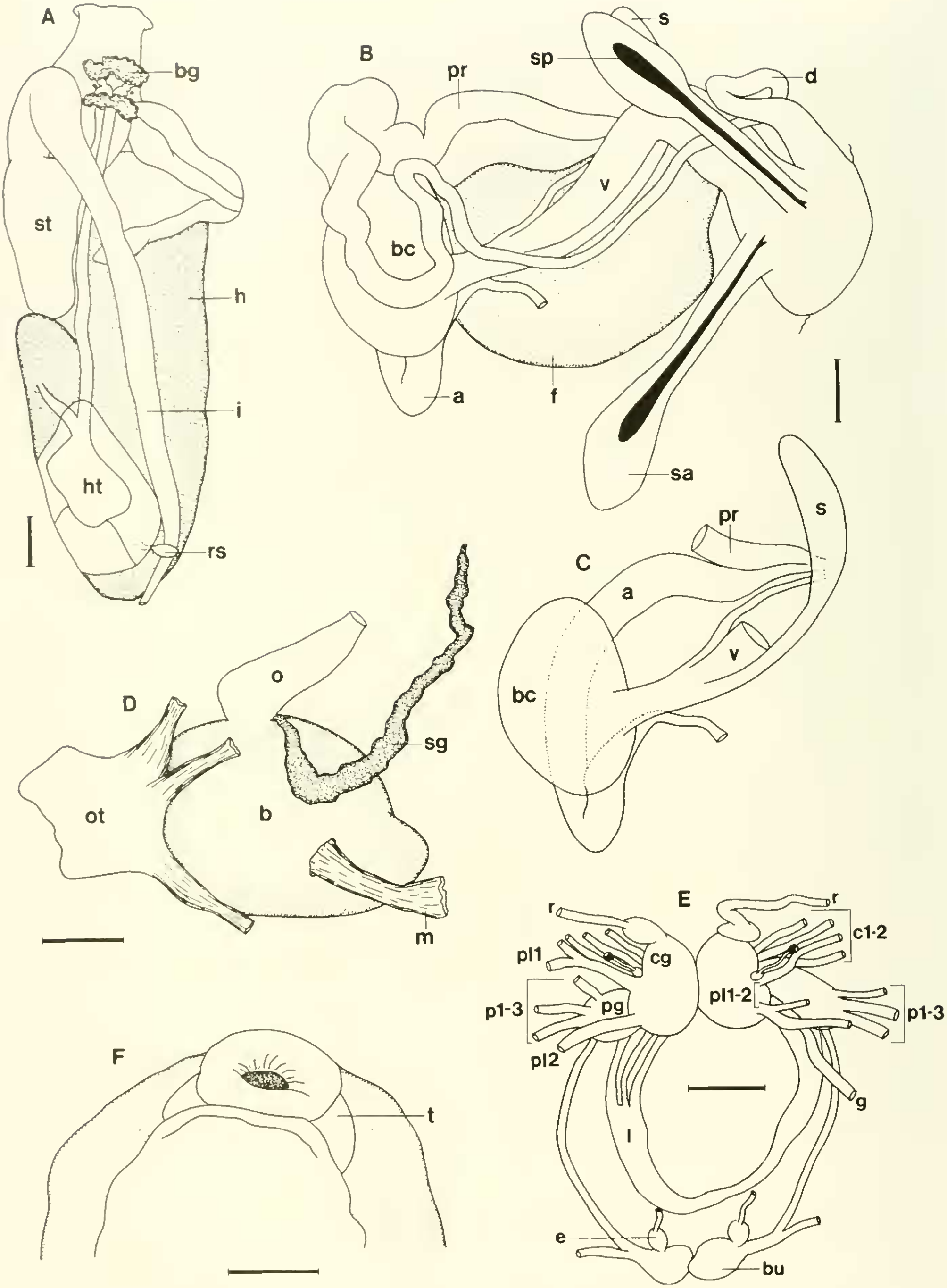

FIG. 18. *Pharodoris diaphora,* new genus and species, paratype from Bathus 1 (stn. CP711). A. Dorsal view of the anatomy; scale bar = 1 mm. B. Reproductive system; scale bar = 0.5 mm. C. Detail of several reproductive organs; scale bar = 0.5 mm. D. Anterior portion of the digestive system; scale bar = 1 mm. E. Central nervous system; scale bar = 0.5 mm. F. Mouth area; scale bar = 1 mm. Abbreviations: a, ampulla; b, buccal bulb; bc, bursa copulatrix; bg, blood gland; bu, buccal ganglion; c, cerebral nerve; cg, cerebral ganglion; d, deferent duct; e, esophageal ganglion; f, female glands; g, genital nerve; h, hermaphrodite and digestive glands; ht, heart; i, intestine; 1, visceral loop; m, retractor muscle; o, esophagus; ot, oral tube; p, pedal nerve; pg, pedal ganglion; pl, pleural nerve; pr, prostate; r, rhinophoral nerve; rs, renal syrinx; s, seminal receptacle; sa, copulatory spine sac; sg, salivary gland; sp, copulatory spine; st, stomach; t, oral tentacle; v, vagina.

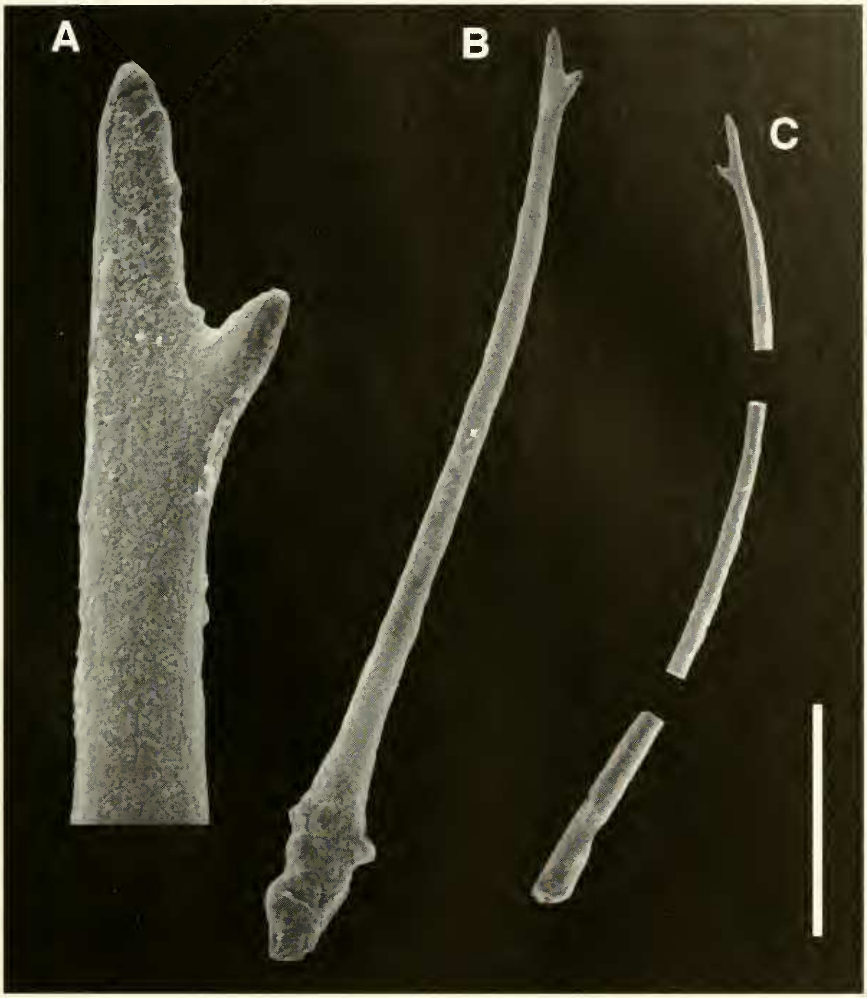

FIG. 19. *Pharodoris,* new genus, copulatory spines. A. *B. philippinensis,* new species, holotype, apex of a spine. B. *B. philippinensis* new species, holotype, general view of a spine. C. *B. diaphora* new species, paratype from Bathus 1 (stn. CP711), general view of a spine, holotype.

truding from the dorsal surface of the tubercles (Fig. 17D). The branchial sheath is very elevated, rising clearly over the dorsal surface of the body. The perfoliate rhinophores are composed of 30 lamellae. There are five bipinnate, very elongate branchial leaves. Ventrally, the oral tentacles consist of two triangular prolongations on each side of the buccal area (Fig. 18F). The anterior border of the foot is grooved but not notched. The mantle margin is narrower than the foot.

Based on the field notes, the background color of the living animals is uniformly white to pale yellow. The rhinophores and gill have the same color as the dorsum.

Three additional specimens of this species, which have not been studied for this paper, have been collected from New Caledonia by Bill Rudman (pers. comm.). His manuscript notes read as follows: mantle with low rounded tubercles, spicules radiating from them; central region (visceral hump) with brown speckling between tubercles and on sides of them; tips of tubercles translucent clear; mantle margin translucent cream with some tubercles ringed in brown but most not; general appearance of brownish visceral hump and narrow translucent cream mantle margin; most remarkable feature is the highly developed tall and rigid gill pocket, same color and tuberculation as dorsum; six simple branchial leaves, translucent clear with white edging. It is clear from this description that these specimens are conspecific with the other material here examined.

Anatomy

The posterior end of the oral tube has six strong retractor muscles (Fig. 18D), which are attached to the body wall. The large, oval, muscular buccal bulb has two additional muscles. Two long salivary glands connect to the buccal bulb at the sides of the esophageal junction. The buccal bulb is four times longer than the oral tube. The labial armature is unarmed. The radular formula is 34 × (39.0.39) in a 16 mm preserved length specimen. The are no rachidian teeth. The inner lateral teeth are hamate, having a single cusp and one denticle on the outer side (Fig. 17A). The teeth increase in size gradually towards the medial portion of the half-row (Figs 17B). The mid-lateral teeth are hamate, with a long cusp, and they lack denticles. The three outermost teeth are very small and have 10–11 small denticles (Fig. 17C). The esophagus is long and connects directly to the stomach (Fig. 18A).

The ampulla is long and convoluted; it narrows into the gonoduct, which branches into a short oviduct and the prostate (Fig. 18C). The oviduct enters the female glands near the nidamental opening. The prostate is tubular and elongate (Fig. 18B); it narrows and expands again into the short deferent duct. The deferent duct opens into a common atrium with the vagina. On the atrium, near the opening of the vagina, there are two large glands, each one containing a bifid, rigid spine about 1 mm long (Figs. 18B, 19C). The penis is unarmed. The vagina is long and wide. At its proximal end, the vagina connects to the large and oval bursa copulatrix. From the medial part of the vagina leads the elongate seminal receptacle and the long uterine duct.

In the central nervous system (Fig. 18E), the cerebral and pleural ganglia are fused and distinct from the pedal ganglia. There are three cerebral nerves leading from each cerebral ganglion, and two pleural nerves lead from each pleural ganglion. The buccal ganglia lie near the rest of the central nervous system, joined to the cerebral ganglia by two long nerves. Gastroesophageal, rhinophoral, and optical ganglia are present. The pedal ganglia are clearly separated, with three nerves leading from each. The pedal and parapedal commissures are enveloped together with the visceral loop along most of their length.

The circulatory system (Fig. 18A) consists of a heart and two blood glands situated in front and behind the central nervous system.

Etymology

From the Ancient Greek *diaphoros* (different), in reference to the strange shape of this animal.

Remarks

Pharodoris diaphora is different from all species of cryptobranch dorids previously described. The characteristic, very elevated branchial sheath is a unique feature of this genus. Internally, the presence of two large glands containing bifid, rigid spines is only present in this genus. For a comparison to other members of this genus, see Remarks on *Pharodoris philippinensis*.

Pharodoris philippinensis Valdés, new species (Figs. 2E, 19A, B, 20, 21)

Material Examined

HOLOTYPE: Philippines, Musorstom 3 Expedition, stn. CP121 (12°08′N, 121°18′E), 73–84 m, 03 June 1985, 19 mm preserved length, dissected, leg. P. Bouchet and M. P. Triclot (MNHN).

External Morphology

The body is somewhat elevated, oval (Fig. 2E). The dorsum is covered with simple, conical tubercles. Some of them, more abundant in the center of the body, are twice as large as the others. The branchial sheath is very elevated, rising clearly over the dorsal surface of the body. The perfoliate rhinophores are each composed of 36 lamellae. There are five bip-

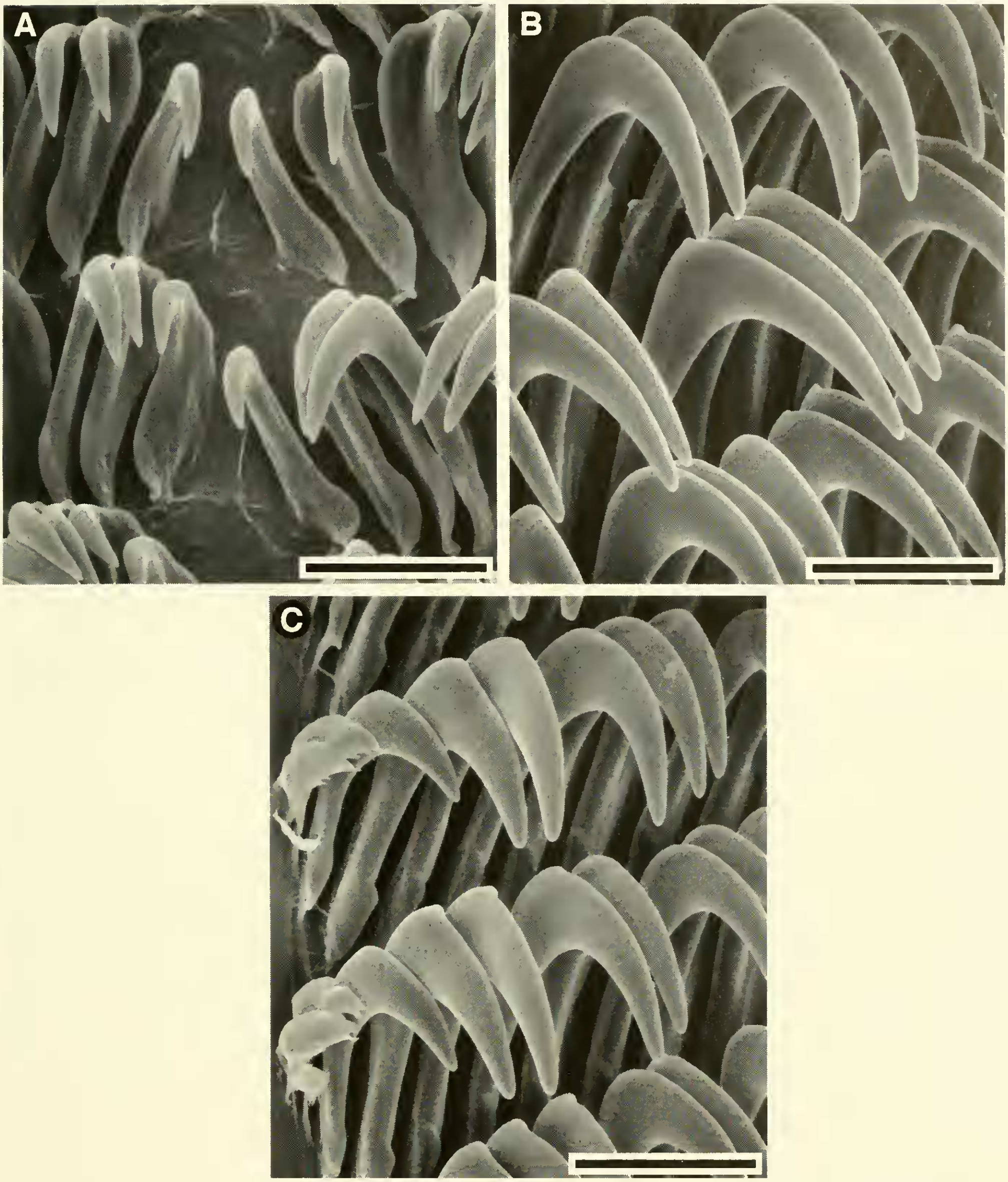

FIG. 20. *Pharodoris philippinensis,* new genus and species, holotype. A. Inner lateral teeth; scale bar = 43 µm. B. Mid-lateral teeth; scale bar = 60 µm. C. Outer lateral teeth; scale bar = 75 µm.

innate, very elongate branchial leaves. Ventrally, the oral tentacles consist of two triangular prolongations on each side of the buccal area. The anterior border of the foot is grooved but not notched. The mantle margin is narrower than the foot.

The color of the living animal is unknown. The preserved specimen is uniformly pale cream.

Anatomy

The labial armature is unarmed. The radular formula is 39 × (44.0.44) in a 19 mm pre-

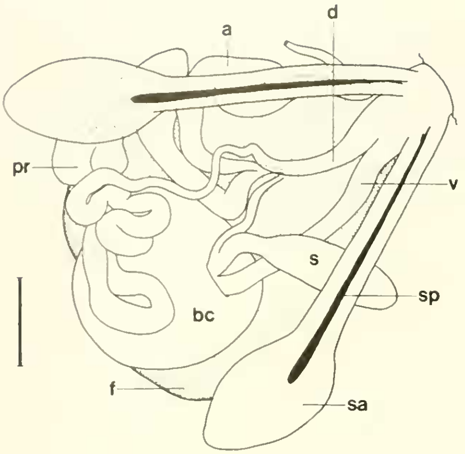

FIG. 21. *Pharodoris philippinensis,* new genus and species, holotype, reproductive system. Abbreviations: a, ampulla; bc, bursa copulatrix; d, deferent duct; f, female glands; pr, prostate; s, seminal receptacle; sa, copulatory spine sac; sp, copulatory spine; v, vagina.

served length specimen. There are no rachidian teeth. The innermost lateral teeth are hamate, having a single cusp, and they lack denticles (Fig. 20A). Some inner lateral teeth may have a small, rounded tubercle on their inner side. The teeth increase in size gradually towards the medial portion of the half-row (Fig. 20B). The mid-lateral teeth are hamate, with a long cusp, and they lack denticles. The three outermost teeth are very small and have 8–10 small denticles (Fig. 20C).

The ampulla is long and convoluted; it narrows into the gonoduct, which branches into a short oviduct and the prostate (Fig. 21). The oviduct enters the female glands near the nidamental opening. The prostate is tubular and elongate; it narrows and expands again into the short deferent duct. The deferent duct opens into a common atrium with the vagina. The atrium has two large glands, each one containing a bifid, rigid spine about 1 mm long (Figs. 19A, B, 21). The penis is unarmed. The vagina is long and wide. At its proximal end, the vagina connects to the large and rounded bursa copulatrix. From the bursa copulatrix leads a short duct that branches into the elongate seminal receptacle and the uterine duct.

Etymology

From the Philippines, the type locality of this species.

Remarks

Pharodoris philippinensis differs from *P. diaphora* in the radula and reproductive system morphology. The innermost lateral teeth of *B. diaphora* have a large denticle that is absent in *B. philippinensis.* Only few inner teeth of *B. philippinensis* have a small, rounded denticle on the inner side, whereas all the inner laterals of *B. diaphora* have a large, conical denticle. From the bursa copulatrix of *B. philippinensis* emerge two ducts, one connecting to the vagina and the other, very short, branching into the seminal receptacle and the uterine duct, whereas in *B. diaphora* a single duct emerges, branching into the vagina, the seminal receptacle and the uterine duct.

Pharodoris sp. (Fig. 22)

Material Examined

Banc Argo, Coral Sea, Musorstom 5 Expedition, stn. 290 (23°06′S, 159°26′E), 300 m, 11 October 1986, 14 mm preserved length, dissected, leg. P. Bouchet, B. Métivier and B. Richer de Forges (MNHN).

External Morphology

The body is somewhat elevated, oval. The dorsum is covered with simple, conical tubercles. Some of them are clearly larger than the others. The branchial sheath is elevated, rising clearly over the dorsal surface of the body. The perfoliate rhinophores are composed of 22 lamellae. There are six bipinnate, very elongate branchial leaves. Ventrally, the oral tentacles consist of two triangular prolongations on each side of the buccal area. The anterior border of the foot is grooved but not notched. The mantle margin is as wide as the foot.

The color of the living animal is unknown. The preserved specimen is uniformly pale cream.

Anatomy

The labial armature is unarmed. The radular formula is 33 × (40.0.40) in a 14 mm preserved length specimen. The are no rachidian teeth. The innermost lateral teeth are hamate, having a single cusp, and they general lack denticles (Fig. 22A). Some inner lateral teeth may have a small, rounded tubercle on their inner side. The teeth increase in size gradu-

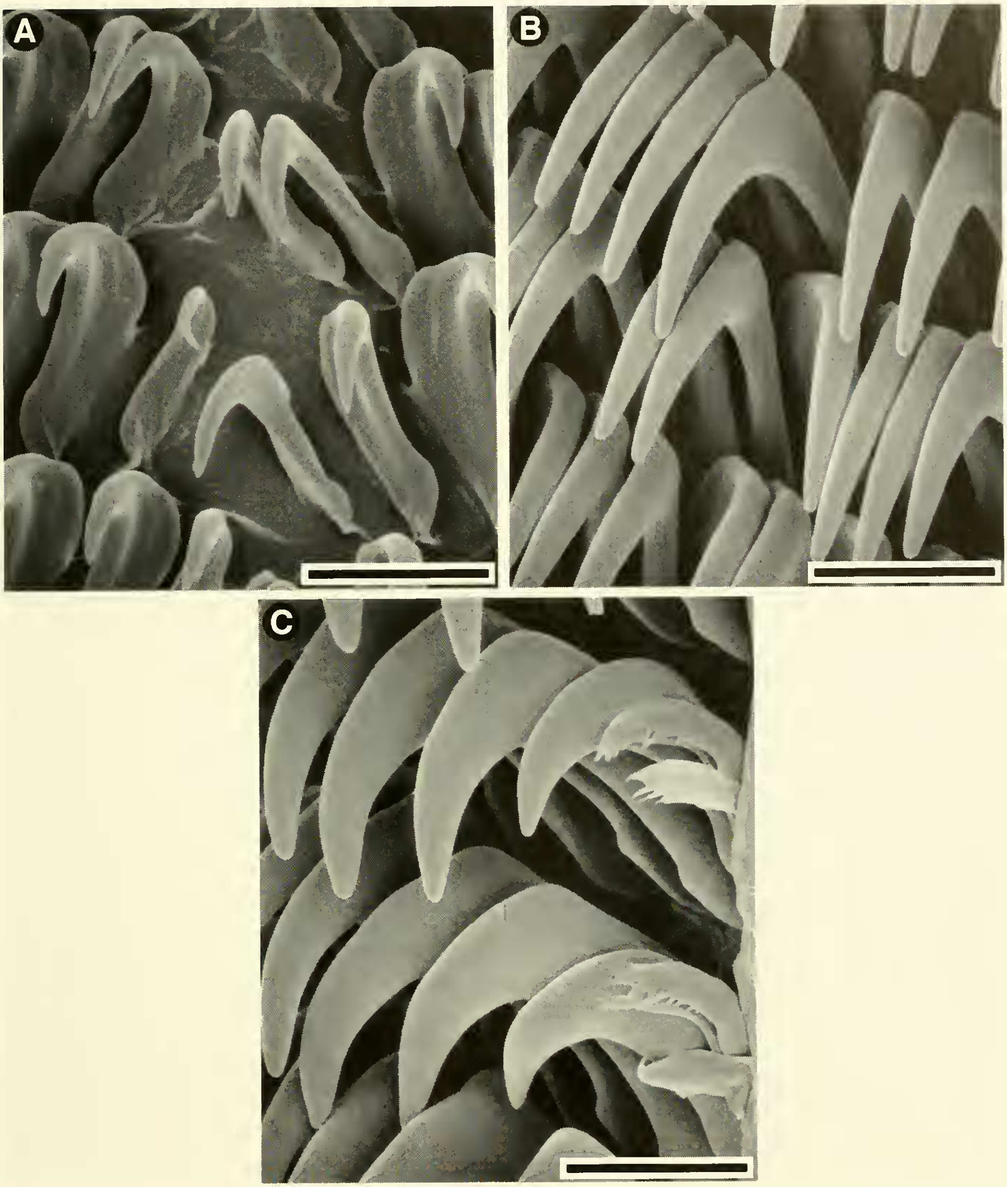

FIG. 22. *Pharodoris* sp., specimen from Musorstom 5 (stn. 290). A. Inner lateral teeth, scale bar = 43 μm. B. Mid-lateral teeth; scale bar = 60 μm. C. Outer lateral teeth; scale bar = 60 μm.

ally towards the medial portion of the half-row (Fig. 22B). The mid-lateral teeth are hamate, with a long cusp, and they lack denticles. The three outermost teeth are very small and have 5–8 small denticles (Fig. 22C).

The single specimen has the reproductive system partially developed. The two large glands associated with the atrium are visible, but some other organs are not discernible.

Remarks

The radula of *Pharodoris* sp. is very similar to that of *Pharodoris philippinensis*. In both, the mid-lateral teeth lack denticles, which are only present in the innermost and outermost lateral teeth. According to the available information, it is very likely that both animals belong to the same species. However, in view of the incomplete development of genital characters for this *Pharodoris* sp., I keep it provisionally separated. Moreover, since there is no information on the reproductive system and the external coloration of *Pharodoris* sp., I will leave it unnamed until more material and information becomes available.

Genus *Geitodoris* Bergh, 1891

Type Species: *Doris complanata* Verrill, 1880, by monotypy.

Geitodoris pallida Valdés, new species
(Figs 2G, 16A, 23, 24)

Material Examined

HOLOTYPE: Norfolk Ridge, New Caledonia, Bathus 3 Expedition, stn. CP833 (21°14′S, 165°55′E), 441-444 m, 30 November 1993, 12 mm preserved length, dissected, leg. P. Bouchet, B. Richer de Forges and A. Warén (MNHN).

External Morphology

The body is elevated and oval (Fig. 2G). The dorsum is covered with irregular tubercles, having a number of spicules projecting all over the surface. There are some larger tubercles (up to 200 μm long) surrounded by smaller tubercles (Fig. 23E). The perfoliate rhinophores are composed of 22 lamellae. There are five unipinnate branchial leaves. Ventrally, the oral tentacles are short and triangular. The anterior border of the foot is notched and grooved (Fig. 24F). The mantle margin is about as wide as the foot.

Based on the field notes, the background color of the living animal is uniformly pale cream. There are several pale brown spots in the mantle margin. The rhinophores and gill have the same color as the dorsum.

Anatomy

The posterior end of the oral tube has six strong retractor muscles (Fig. 24D), which are attached to the body wall. The small, oval, muscular buccal bulb has two additional muscles. The buccal bulb is ten times shorter than the oral tube. The jaws consist of numerous thin, unicuspid elements about 30 μm long (Fig. 23D). The radular formula is 18 × (23.0.23) in a 12 mm preserved length specimen. There are no rachidian teeth. The inner lateral teeth are hamate, having a single cusp, and they lack denticles (Fig. 23A). The teeth increase in size gradually towards the medial portion of the half-row (Fig. 23B). The outermost teeth are elongate plates with number of small denticles (Fig. 23C). The esophagus is long and connects directly to the intestine.

The ampulla is long; it narrows into the gonoduct, which branches into a short oviduct and the prostate (Fig. 24C). The oviduct enters the female glands near the center of the mass. The prostate is flattened and granular (Fig 24B); it is divided into two portions that are clearly distinguishable by their different texture and coloration. The largest portion is pale yellow and connects to the deferent duct, whereas the smallest portion is whitish and connects to the ampulla. The deferent duct is very long and narrow. It narrows and expands again into the short ejaculatory portion. The deferent duct opens into a common atrium with the vagina. The penis is unarmed. There is an accessory gland connected to the atrium, which has several rigid structures inside. These structures are elongate, about 150 μm long (Fig 16A). The vagina is long and folded. At its proximal end, the vagina connects to the large and irregular bursa copulatrix. From the bursa copulatrix leads another long and convoluted duct that connects to the seminal receptacle and the uterine duct. The bursa copulatrix is about four times larger than the seminal receptacle.

In the central nervous system (Fig. 24E), the cerebral and pleural ganglia are largely fused and distinct from the pedal ganglia. There are four cerebral nerves leading from each cerebral ganglion, and three pleural nerves lead from each pleural ganglion. The buccal ganglia lie near the rest of the central nervous system, joined to the cerebral ganglia by two long nerves. Gastroesophageal, rhinophoral, and optical ganglia are present. The pedal ganglia are clearly separated, with two nerves leading from each. The pedal and parapedal commissures are enveloped together with the visceral loop along all their length.

The circulatory system (Fig. 24A) consists of a heart and two blood gland situated in front and behind the central nervous system.

Etymology

From the Latin *pallidus* (pale), in reference to the color of this species.

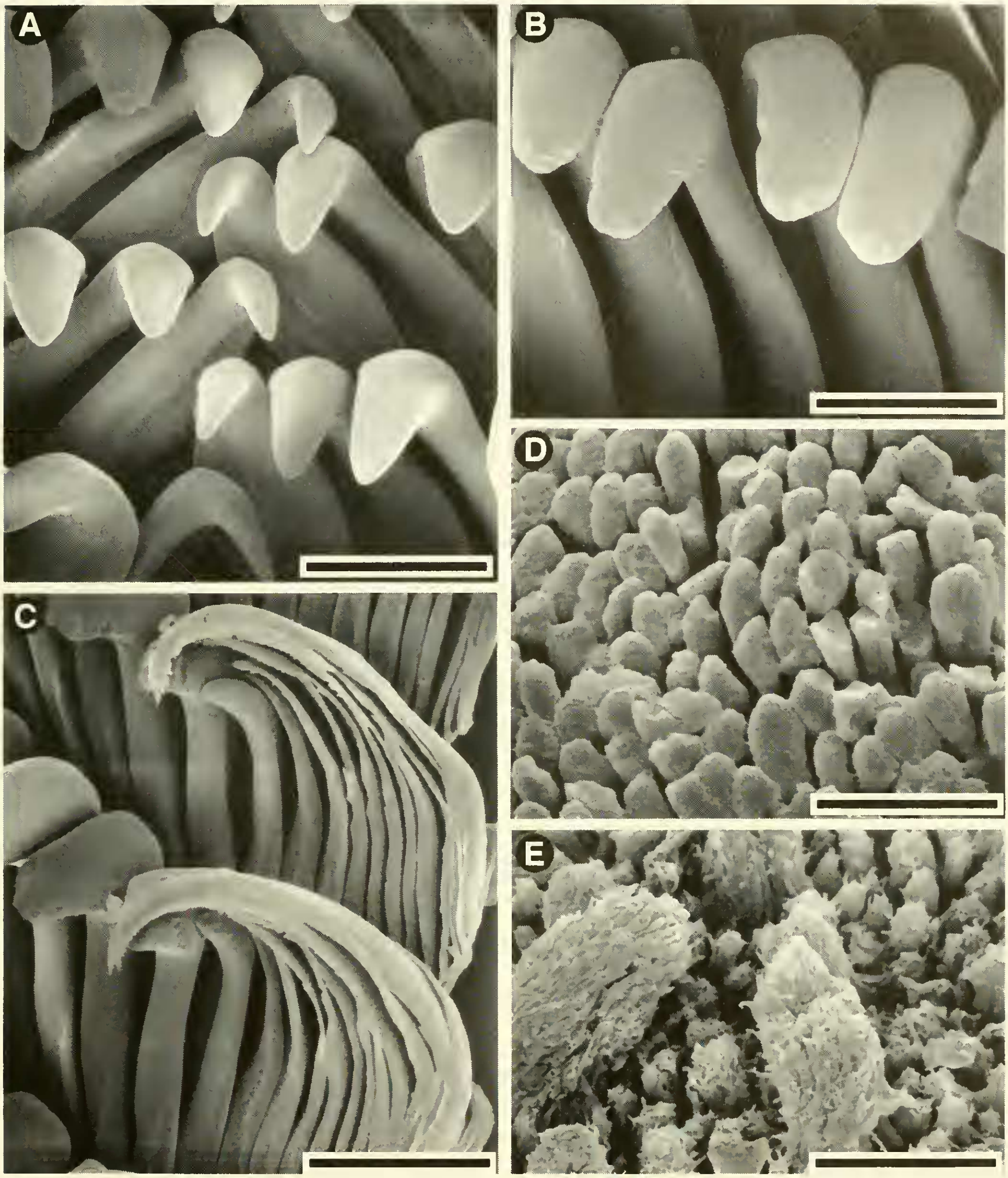

FIG. 23. *Geitodoris pallida*, new species, holotype. A. Inner lateral teeth; scale bar = 75 μm. B. Mid-lateral teeth; scale bar = 60 μm. C. Outer lateral teeth; scale bar = 75 μm. D. Jaw elements; scale bar = 25 μm. E. Dorsal tubercles; scale bar = 150 μm.

Remarks

Geitodoris pallida clearly belongs to the genus *Geitodoris* in having the following combination of characters: anterior border of the foot notched and grooved, dorsal tubercles simple, presence of jaws, radula lacking rachidian teeth, inner lateral teeth hamate, outermost lateral teeth elongate, plate-like, prostate flattened, penis and vagina unarmed, presence of an accessory gland.

This new species is characterized by the

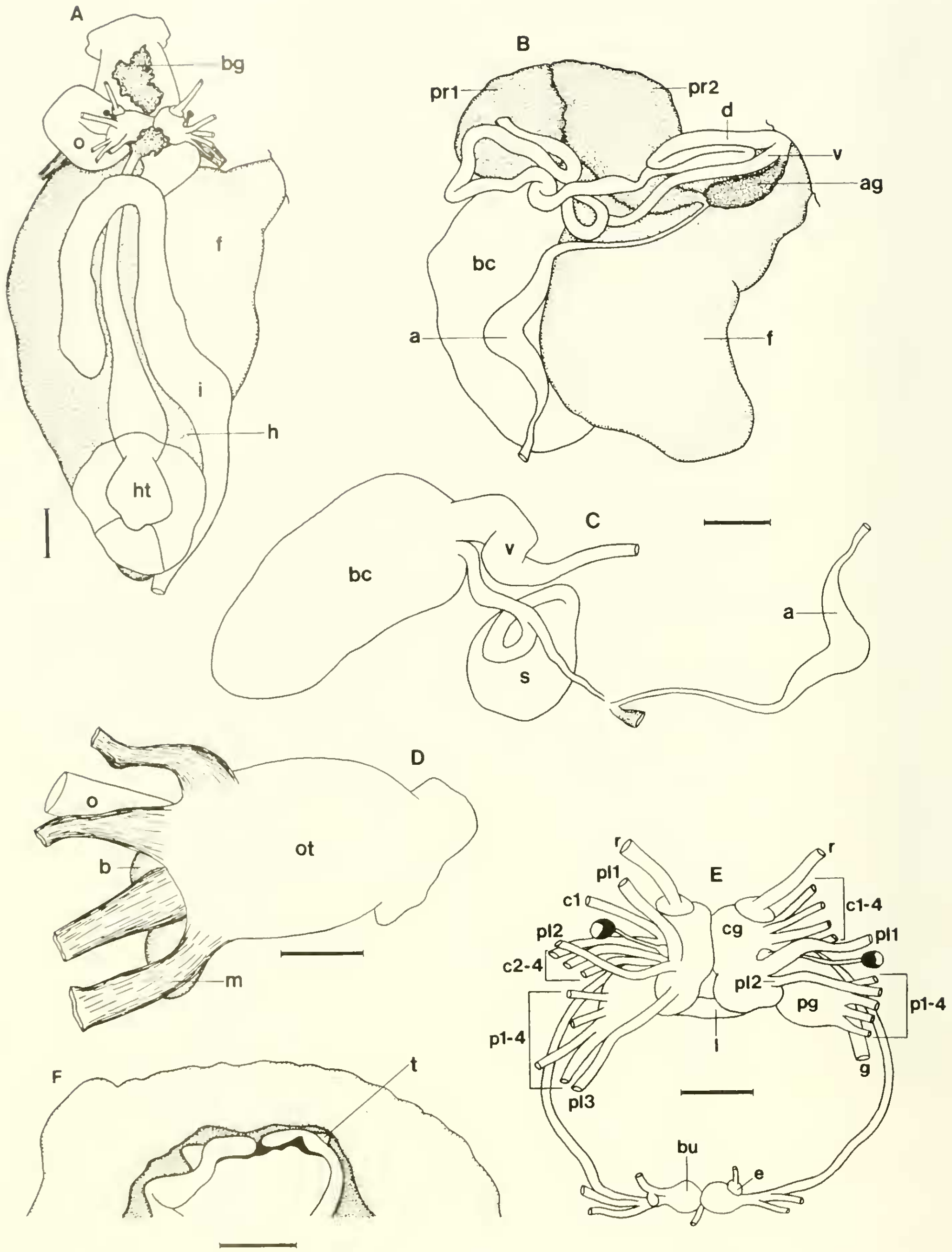

FIG. 24. *Geitodoris pallida*, new species, holotype. A. Dorsal view of the anatomy; scale bar = 1 mm. B. Reproductive system; scale bar = 0.5 mm. C. Detail of several reproductive organs; scale bar = 0.5 mm. D. Anterior portion of the digestive system; scale bar = 1 mm. E. Central nervous system; scale bar = 0.5 mm. F. Mouth area; scale bar = 1 mm. Abbreviations: a, ampulla; ag, accessory gland; b, buccal bulb; bc, bursa copulatrix; bg, blood gland; bu, buccal ganglion; c, cerebral nerve; cg, cerebral ganglion; d, deferent duct; e, esophageal ganglion; f, female glands; g, genital nerve; h, hermaphrodite and digestive glands; ht, heart; i, intestine; l, visceral loop; m, retractor muscle; o, esophagus; ot, oral tube; p, pedal nerve; pg, pedal ganglion; pl, pleural nerve; pr, prostate; r, rhinophoral nerve; s, seminal receptacle; t, oral tentacle; v, vagina.

presence of several solid structures, probably copulatory spines, in the accessory gland. The only described species of the genus with these structures is *Geitodoris pusae* (Er. Marcus, 1955) described from southern Brazil. According to Er. Marcus (1955), *G. pusae* has a denticle on the inner side of the innermost lateral teeth, whereas it is absent in *G. pallida*. Another difference between these species is that the outermost lateral teeth of *G. pallida* have a number of small denticles that appear to be absent in *G. pusae*. In addition, the outermost teeth of *G. pusae* are much longer than the mid-laterals, whereas in *G. pallida* they are shorter.

Other Pacific species of *Geitodoris* with a proximal geographic range are *G. ohshimai* Baba, 1936, and *G. lutea* Baba, 1937, from Japan, and *G. sticta* Miller, 1996, from New Zealand. *Geitodoris ohshimai* is clearly distinguishable from *G. pallida* in having denticles on the mid-lateral teeth (Baba, 1936). *Geitodoris lutea* has the outermost lateral teeth very elongate, longer than the mid-laterals and smooth (Baba, 1937), whereas in *G. pallida* they are shorter than the mid-laterals and bear numerous small denticles. *Geitodoris sticta* has short outermost lateral teeth with denticles, but in this species there are few, irregular denticles on the outer side of the cusp (Miller, 1996), whereas in *G. pallida* there are numerous, regularly arranged denticles on the inner side of the cusp. In addition, the reproductive system of *G. sticta* lacks an accessory gland that is present in *G. pallida*.

Miller (1996) regarded the Australian species *Discodoris palma* Allan, 1932, and *D. crawfordi* Burn, 1969, as belonging to *Geitodoris*. According to the redescription of *D. palma* by Thompson (1975), this species has very elongate, smooth outer lateral teeth, which contrast with the short, denticulate outer laterals of *G. pallida*. The outer radular teeth of *D. crawfordi* are short and hamate (Burn, 1969), more similar to those of the genus *Discodoris*, and it is very likely that it belongs in this latter genus. Unfortunately, the reproductive system of neither of these species has been described, so comparisons of the morphology of the genital organs is not possible.

Genus *Discodoris* Bergh, 1877

Type Species: *Discodoris boholiensis* Bergh, 1877, by subsequent designation by O'-Donoghue (1926).

Discodoris sp. (Figs. 2I, 25, 26)

Material Examined

North of New Caledonia, Bathus 4 Expedition, stn. CP910 (18°59′S, 163°09′E), 560–608 m, 05 September 1994, 66 mm preserved length, leg. B. Métivier and B. Richer de Forges (MNHN).

External Morphology

The body is elevated and oval (Fig. 2I). The dorsum is covered with simple, elongate tubercles, all of them about 200 µm long (Fig. 25E). The perfoliate rhinophores are composed of 35 lamellae. There are five bipinnate branchial leaves. The rhinophoral and branchial sheaths are somewhat elevated, bearing numerous tubercles. Ventrally, the oral tentacles are short and conical. The anterior border of the foot is notched and grooved (Fig. 26F). The mantle margin is narrower than the foot.

The color of the living animals is unknown. The preserved specimen is uniformly pale cream. The rhinophores and gill have the same color as the dorsum.

Anatomy

The posterior end of the oral tube has six strong retractor muscles (Fig. 26D), which are attached to the body wall. The oval, muscular buccal bulb has two additional muscles. The oral tube is about twice as long as the buccal bulb. The jaws consist of numerous irregular elements, about 15 µm long (Fig. 25D). The radular formula is 21 × (25.0.25) in a 66 mm preserved length specimen. There are no rachidian teeth. The inner lateral teeth are hamate, having a single cusp, and they lack denticles (Fig. 25A). The teeth increase in size gradually towards the medial portion of the half-row (Fig. 25A, B). The outermost teeth are also hamate and lack denticles (Fig. 25C). The esophagus is very long, convoluted and connects directly to the stomach.

The ampulla is very long and convoluted; it narrows into the gonoduct, which branches into a short oviduct and the prostate (Fig. 26B). The oviduct enters the female glands near the nidamental opening. The prostate is elongate and granular; it narrows and expands again into the long, wide and muscular deferent duct. The deferent duct opens into a

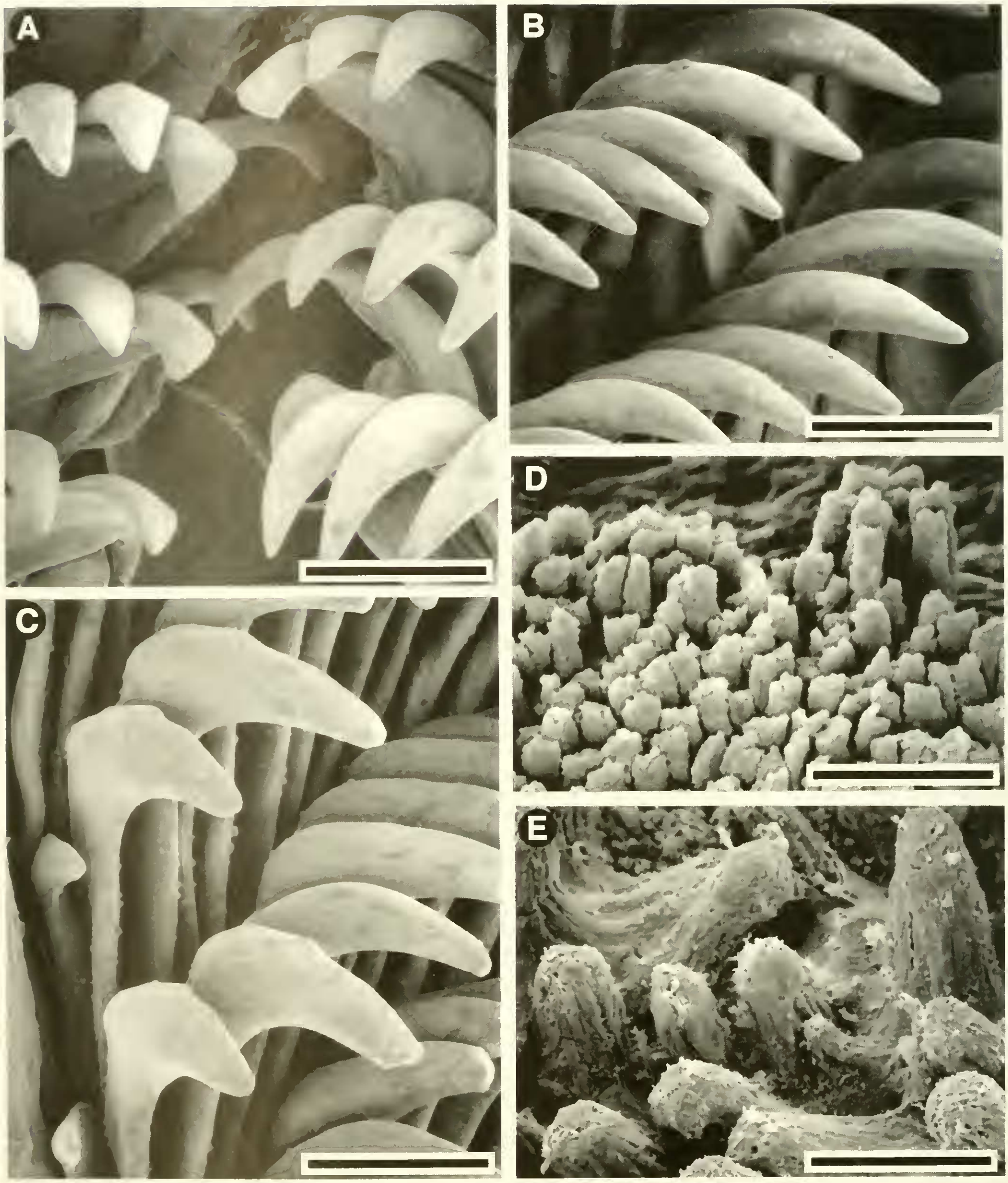

FIG. 25. *Discodoris* sp. A. Inner lateral teeth; scale bar = 200 μm. B. Mid-lateral teeth; scale bar = 150 μm. C. Outer lateral teeth; scale bar = 150 μm. D. Jaw elements; scale bar = 25 μm. E. Dorsal tubercles; scale bar = 250 μm.

common atrium with the vagina. The penis is unarmed. The vagina is very wide; at its proximal end, it connects to the large and oval bursa copulatrix. From the vagina leads another long duct that connects to the seminal receptacle and the very long uterine duct (Fig. 26C). The bursa copulatrix is about the same size as the seminal receptacle.

In the central nervous system (Fig. 26E), the cerebral and pleural ganglia are fused and distinct from the pedal ganglia. There are three cerebral nerves leading from each cerebral ganglion, and two pleural nerves lead from each pleural ganglion. The buccal ganglia lie near the rest of the central nervous system, joined to the cerebral ganglia by two

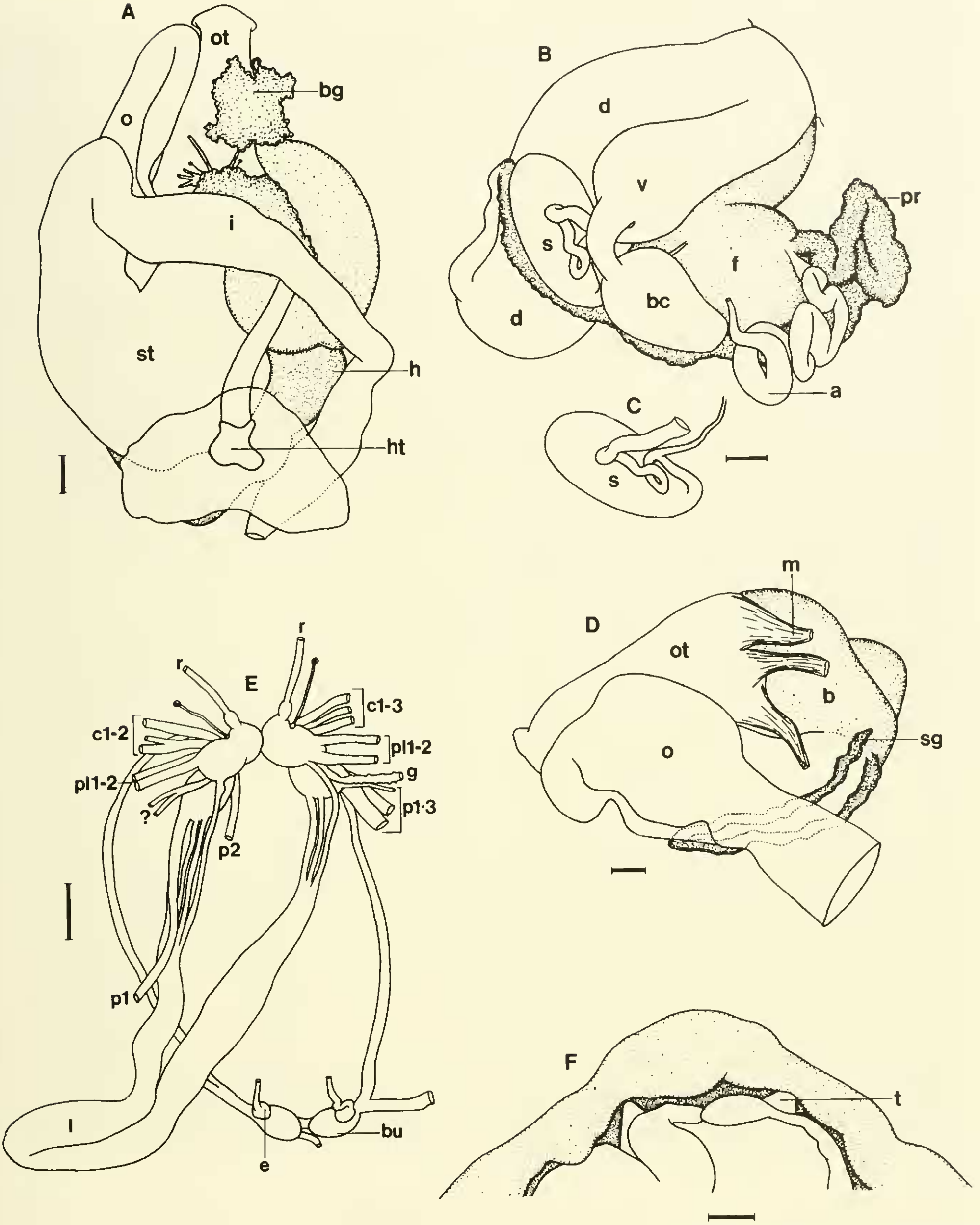

FIG. 26. *Discodoris* sp. A. Dorsal view of the anatomy; scale bar = 2 mm. B. Reproductive system; scale bar = 1 mm. C. Detail of the seminal receptacle; scale bar = 1 mm. D. Anterior portion of the digestive system; scale bar = 1 mm. E. Central nervous system; scale bar = 1 mm. F. Mouth area; scale bar = 2 mm. Abbreviations: a, ampulla; b, buccal bulb; bc, bursa copulatrix; bg, blood gland; bu, buccal ganglion; c, cerebral nerve; d, deferent duct; e, esophageal ganglion; f, female glands; g, genital nerve; h, hermaphrodite and digestive glands; ht, heart; i, intestine; l, visceral loop; m, retractor muscle; o, esophagus; ot, oral tube; p, pedal nerve; pl, pleural nerve; pr, prostate; r, rhinophoral nerve; s, seminal receptacle; sg, salivary gland; st, stomach; t, oral tentacle; v, vagina.

long nerves. Gastroesophageal, rhinophoral, and optical ganglia are present. The pedal ganglia are clearly separated, with two nerves leading from each. The pedal and parapedal commissures are enveloped together with the visceral loop along most of their length.

The circulatory system (Fig. 26A) consists of a heart and two blood glands situated in front and behind the central nervous system.

Remarks

This species clearly belongs to the genus *Discodoris* as indicated by the presence of the following characters: dorsum covered with simple tubercles, presence of jaws, radula with hamate, smooth teeth, absence of accessory gland and penis, and vagina unarmed. Other features of the genus *Discodoris* present in this species are foot notched and grooved, oval digitiform tentacles and prostate flattened.

Numerous species have been assigned to the genus *Discodoris,* most of them from Indo-Pacific tropical waters, but also from temperate and cold regions. *Discodoris* sp. is the first species described from deep waters. The long vagina of this species appears to distinguish it from other members of the genus, but the lack of anatomical studies in most members of *Discodoris* makes difficult comparison with this new species. Considering that only one specimen of this species is available and its external coloration is unknown, I prefer not to name this species until additional material becomes available.

Discodoris achroma Valdés, new species
(Figs. 2H, 27, 28)

Material Examined

HOLOTYPE: New Caledonia, Musorstom 4 Expedition, stn. CC245 (22°07′S, 167°11′E), 415–435 m, 05 October 1985, 15 mm preserved length, leg. P. Bouchet and B. Richer de Forges (MNHN).

PARATYPES: New Caledonia, Biocal Expedition, stn. CP109 (22°11′S, 167°16′E), 495–515 m, 09 September 1985, one specimen 12 mm preserved length, dissected, leg. P. Bouchet, B. Métivier and B. Richer de Forges (CASIZ 121098). New Caledonia, Musorstom 4 Expedition, stn. CP242 (22°06′S, 167°10′E), 500–550 m, 03 October 1985, one specimen 11 mm preserved length, dissected, leg. P. Bouchet and B. Richer de Forges (MNHN). Norfolk Ridge, New Caledonia, Bathus 3 Expedition, stn. CP832 (23°03′S, 166°54′E), 650–659 m, 30 November 1993, one specimen 13 mm preserved length, dissected, leg. P. Bouchet, B. Richer de Forges and A. Warén (MNHN).

ADDITIONAL MATERIAL: Coral Sea, Musorstom 5 Expedition, stn. 323 (21°13′S, 157°58′E), 970 m, 14 October 1986, 15 mm preserved length, leg. P. Bouchet, B. Métivier and B. Richer de Forges (MNHN).

External Morphology

The body is elevated and oval (Fig. 2H). The dorsum is covered with simple, conical tubercles, all of them about 100 μm long (Fig. 27E). The perfoliate rhinophores are composed of 33 lamellae. There are five bipinnate branchial leaves. The rhinophoral and branchial sheaths are somewhat elevated, bearing numerous tubercles. Ventrally, the oral tentacles are conical. The anterior border of the foot is notched and grooved (Fig. 28E). The mantle margin is wider than the foot.

Based on the field notes, the color of the living animals is uniform translucent white. The rhinophores and gill have the same color as the dorsum.

Anatomy

The posterior end of the oral tube has six strong retractor muscles (Fig. 28C), which are attached to the body wall. The oval, muscular buccal bulb has two additional muscles. The oral tube is about twice as long as the buccal bulb. The jaws consist of numerous irregular elements about 50 μm long (Fig. 27D). The radular formula is 15 × (18.0.18) in a 11 mm preserved length specimen and 16 × (18.0.18) in a 13 mm preserved length specimen. There are no rachidian teeth. The inner lateral teeth are hamate, having a small cusp, and they lack denticles (Fig. 27A). The teeth increase in size gradually towards the medial portion of the half-row (Figs. 27A, B). The outermost teeth are also hamate and lack denticles (Fig. 27C). The esophagus is very long, convoluted and connects directly to the large stomach (Fig. 28A).

The ampulla is very short and simple; it narrows into the gonoduct, which branches into a short oviduct and the prostate (Fig. 28B). The oviduct enters the female glands near the

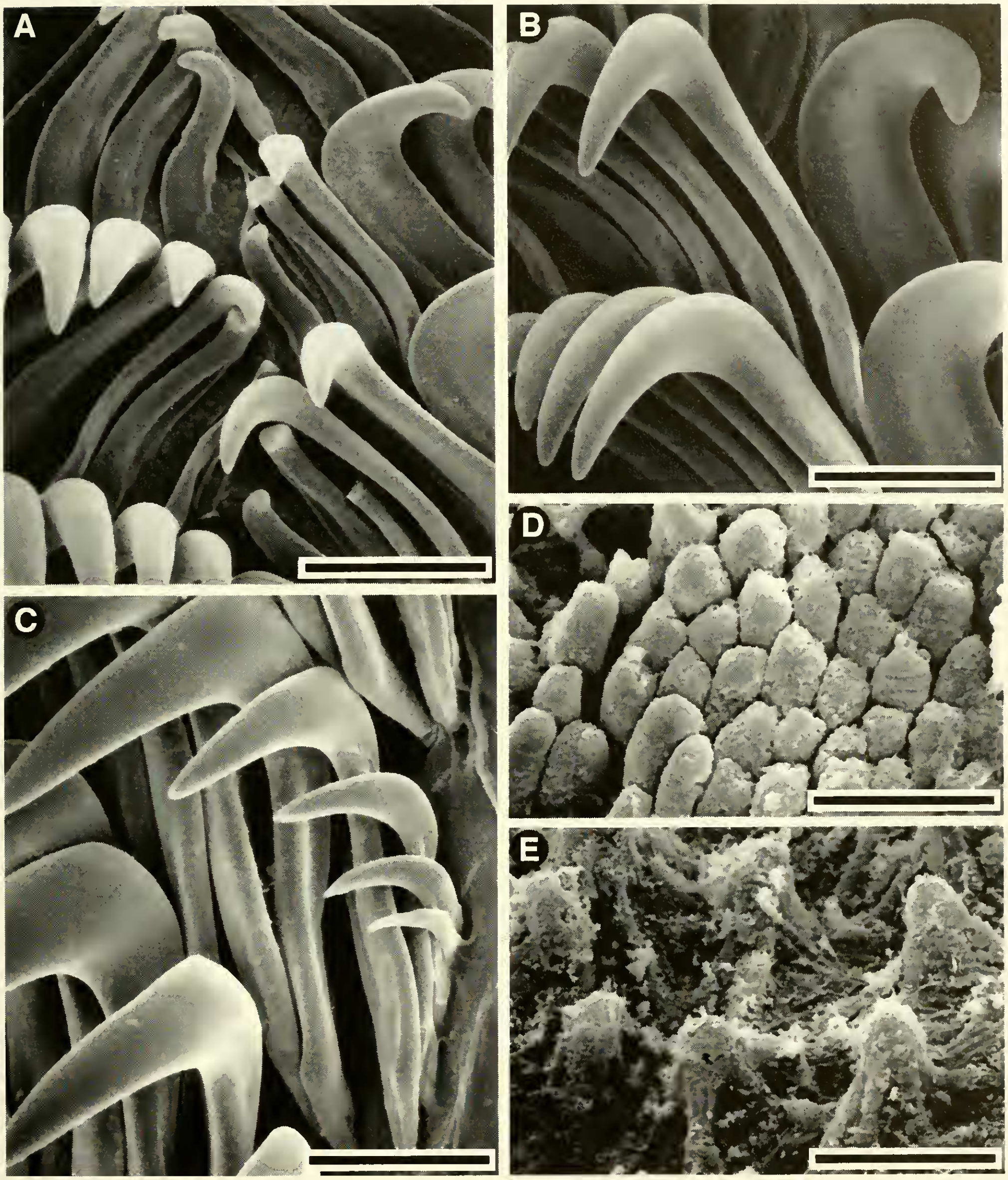

FIG. 27. *Discodoris achroma,* new species, paratype from Musorstom 4 (stn. CP242). A. Inner lateral teeth; scale bar = 60 μm. B. Mid-lateral teeth; scale bar = 60 μm. C. Outer lateral teeth; scale bar = 43 μm. D. Jaw elements; scale bar = 15 μm. E. Dorsal tubercles; scale bar = 100 μm.

center of the mass. The prostate is very elongate and not flattened; it narrows and expands again into the short, muscular deferent duct. The deferent duct opens into a common atrium with the vagina. The penis is unarmed. The vagina is very elongate and convoluted; at its proximal end, it connects to the rounded bursa copulatrix. From the vagina leads another long duct that connects to the seminal receptacle and the uterine duct. The bursa copulatrix is twice as large as the seminal receptacle.

In the central nervous system (Fig. 28D), the cerebral and pleural ganglia are fused and

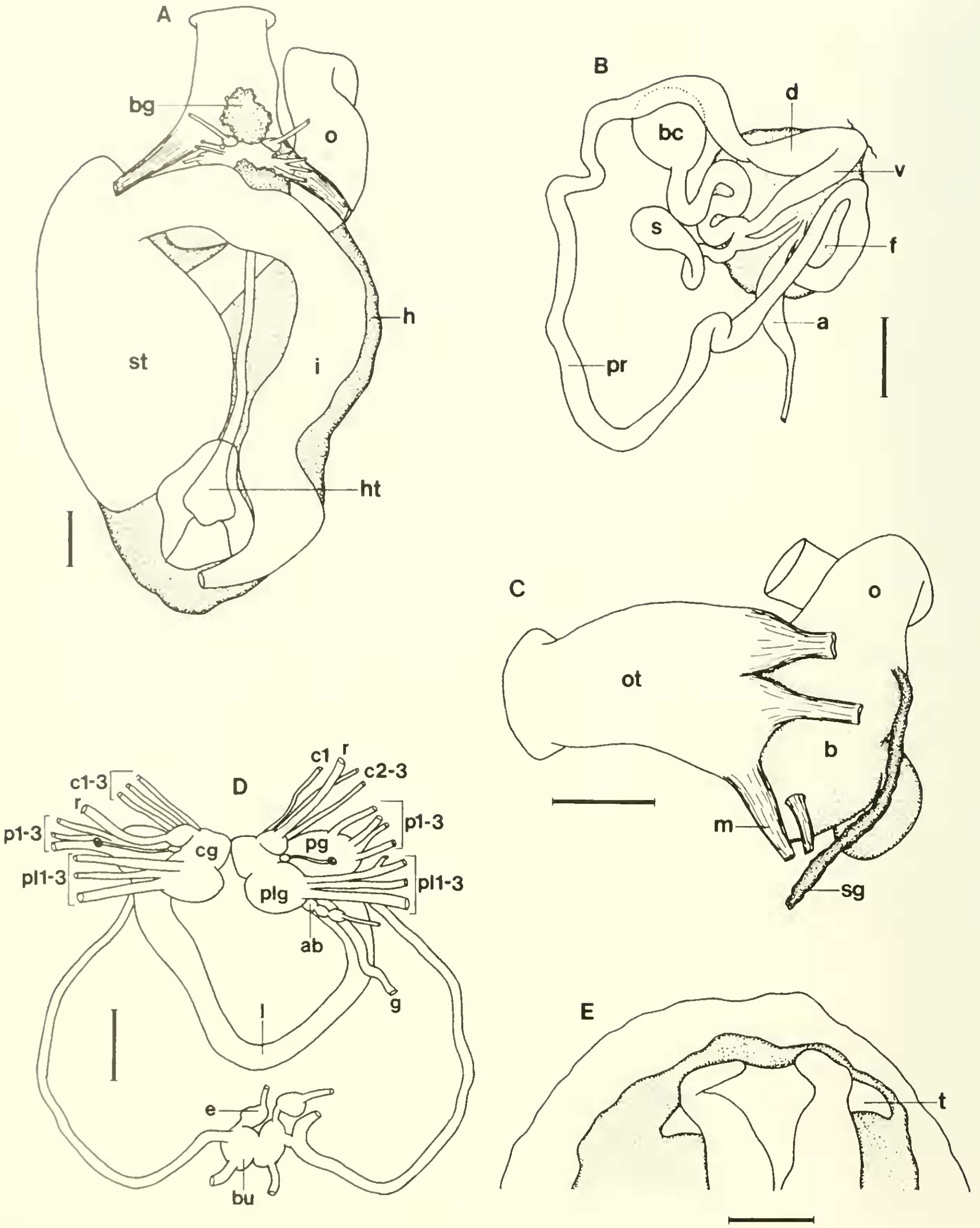

FIG. 28. *Discodoris achroma*, new species, paratype from Bathus 3 (stn. CP832). A. Dorsal view of the anatomy; scale bar = 1 mm. B. Reproductive system; scale bar = 0.25 mm. C. Anterior portion of the digestive system; scale bar = 1 mm. D. Central nervous system; scale bar = 0.5 mm. E. Mouth area; scale bar = 1 mm. Abbreviations: a, ampulla; ab, abdominal ganglion; b, buccal bulb; bc, bursa copulatrix; bg, blood gland; bu, buccal ganglion; c, cerebral nerve; cg, cerebral ganglion; d, deferent duct; e, esophageal ganglion; f, female glands; g, genital nerve; h, hermaphrodite and digestive glands; ht, heart; i, intestine; l, visceral loop; m, retractor muscle; o, esophagus; ot, oral tube; p, pedal nerve; pg, pedal ganglion; pl, pleural nerve; plg, pleural ganglion; pr, prostate; r, rhinophoral nerve; s, seminal receptacle; sg, salivary gland; st, stomach; t, oral tentacle; v, vagina.

distinct from the pedal ganglia. There are three cerebral nerves leading from each cerebral ganglion, and three pleural nerves lead from each pleural ganglion. The buccal ganglia lie near the rest of the central nervous system, joined to the cerebral ganglia by two long nerves. Gastroesophageal, rhinophoral, and optical ganglia are present. The pedal ganglia are clearly separated, with three nerves leading from each. The pedal and parapedal commissures are enveloped together with the visceral loop along all their length. There are three abdominal ganglia on the right side of the visceral loop.

The circulatory system (Fig. 28A) consists of a heart and two blood glands situated in front and behind the central nervous system.

Etymology

From the Ancient Greek *achromos* (lacking color), in reference to the translucent white appearance of this species.

Remarks

This species clearly belongs to the genus *Discodoris* by the presence of the following characters: dorsum covered with simple tubercles, presence of jaws, radula with hamate, smooth teeth, absence of accessory gland and penis, and vagina unarmed. It differs from other shallow-water members of the genus in having a translucent white coloration and lacking a flattened prostate.

Discodoris achroma differs from *Discodoris* sp. in both the external morphology and anatomy. *Discodoris achroma* is a small, translucent species, whereas *Discodoris* sp. is large and uniformly cream. Internally, they differ in the shape of the radular teeth. The innermost lateral teeth of *D. achroma* are longer and have a shorter cusp. The outermost teeth are thinner and comparatively smaller in *D. achroma* than in *Discodoris* sp. The reproductive system of *D. achroma* has the bursa copulatrix connected to the vagina by a long, convoluted duct, whereas in *Discodoris* sp. this duct is much wider and shorter. The uterine duct of *Discodoris* sp. connects near the seminal receptacle, instead of near the bursa copulatrix insertion, as in *D. achroma.* The ampulla of *D. achroma* is short and simple, being very long and convoluted in *Discodoris* sp.

The specimen from the Coral Sea was very poorly preserved and a definitive identification is not possible. The radula is very similar to that of the New Caledonia specimens of *D. achroma,* and it is therefore included in this species.

Genus *Peltodoris* Bergh, 1880

Type Species: *Peltodoris atromaculata* Bergh, 1880, by subsequent designation by O'-Donoghue (1929).

Peltodoris lippa Valdés new species (Figs. 29A, 30, 31)

Material Examined

HOLOTYPE: Vanuatu, Musorstom 8 Expedition, stn. CP1132 (15°38′S, 167°03′E), 161–182 m, 11 October 1994, 23 mm preserved length, leg. P. Bouchet and B. Richer de Forges (MNHN).

External Morphology

The body is flat and oval (29A). The dorsum is covered with simple, conical tubercles. Some tubercles are clearly larger than others and can reach over 200 μm long (Fig. 30D). The perfoliate rhinophores are composed of 16 lamellae. There are six tripinnate branchial leaves. The rhinophoral and branchial sheaths are low and bear numerous tubercles. Ventrally, the oral tentacles are conical. The anterior border of the foot is notched and grooved (Fig. 31E). The mantle margin is as wide as the foot.

Based on the field notes, the color of the living animal is uniform translucent white. The rhinophores and gill have the same color as the dorsum.

Anatomy

The posterior end of the oral tube has six strong retractor muscles (Fig. 31D), which are attached to the body wall. The oval, muscular buccal bulb has two large additional muscles. The oral tube is about twice as long as the buccal bulb. The labial cuticle is smooth. The radular formula is 15 × (31.0.31) in a 23 mm preserved length specimen. There are no rachidian teeth. The inner lateral teeth are hamate, having a small cusp, and they lack denticles (Fig. 30A). The teeth increase in size gradually towards the medial portion of the half-row (Fig. 30A, B). The outermost teeth

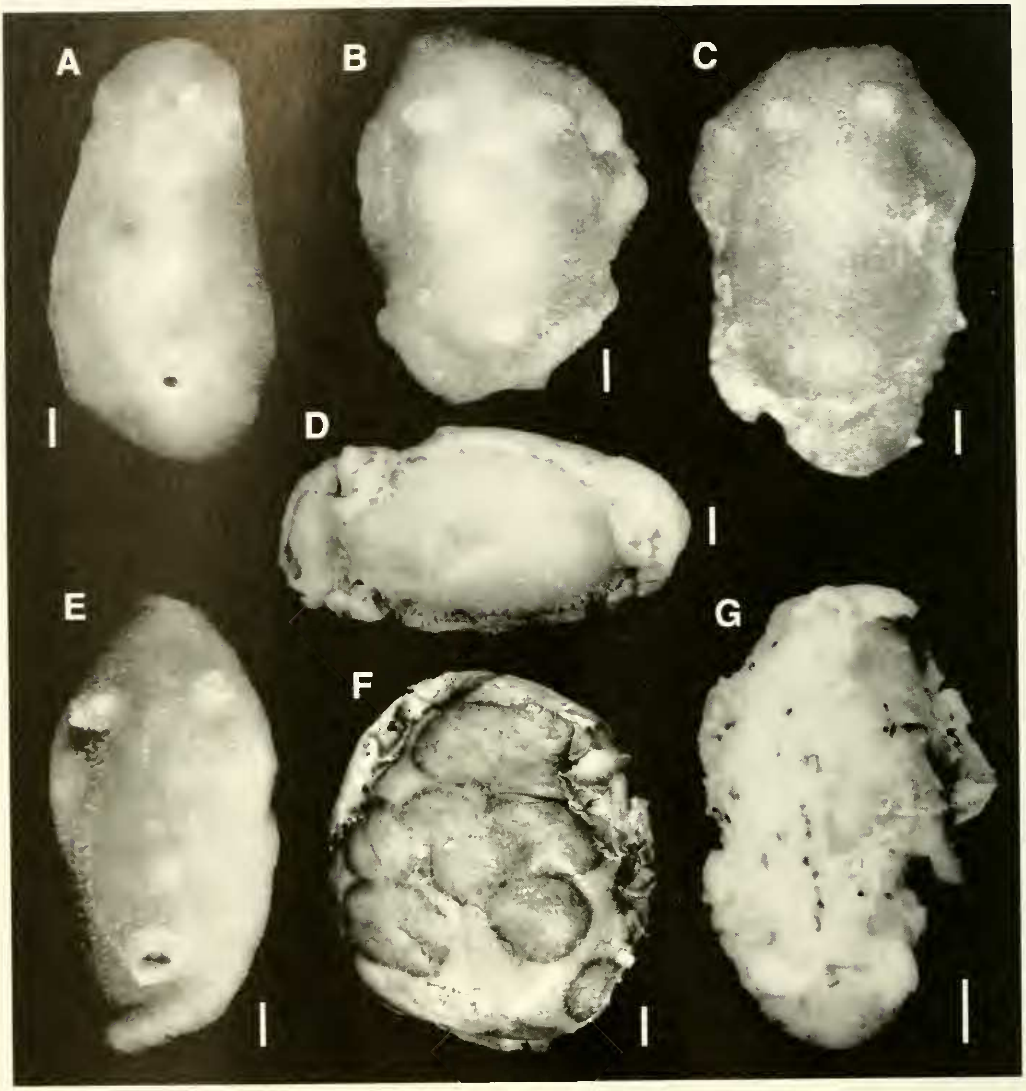

FIG. 29. Preserved specimens. A. *Peltodoris lippa,* new species, holotype; scale bar = 2 mm. B. *Rostanga ankyra,* new species, holotype; scale bar = 1 mm. C. *Diaulula immaculata,* new species, holotype; scale bar = 2 mm. D. *Baptodoris phinei,* new species, holotype; scale bar = 2 mm. E. *Diaulula cerebralis,* new species, paratype from Musorstom 3 (stn. CP128); scale bar = 3 mm. F. *Dendrodoris orbicularis,* new species, holotype; scale bar = 5 mm. G. *Sclerodoris virgulata* new species, holotype; scale bar = 2 mm.

are also hamate and have several, small denticles (Fig. 30C). The esophagus is very long, convoluted and connects directly to the large stomach.

The ampulla is very short and simple; it narrows into the gonoduct, which branches into a short oviduct and the prostate (Fig. 31C). The prostate is flattened, large and granular (Fig 31B); it is divided into two portions that are clearly distinguishable by their different texture and coloration. The deferent duct opens into a common atrium with the vagina. The penis is unarmed. The vagina is very elongate and convoluted; at its proximal end, it connects to the oval bursa copulatrix. From the bursa copulatrix leads another duct that connects to the seminal receptacle and the uterine duct. The bursa copulatrix is twice as large as the seminal receptacle.

In the central nervous system (Fig. 31F),

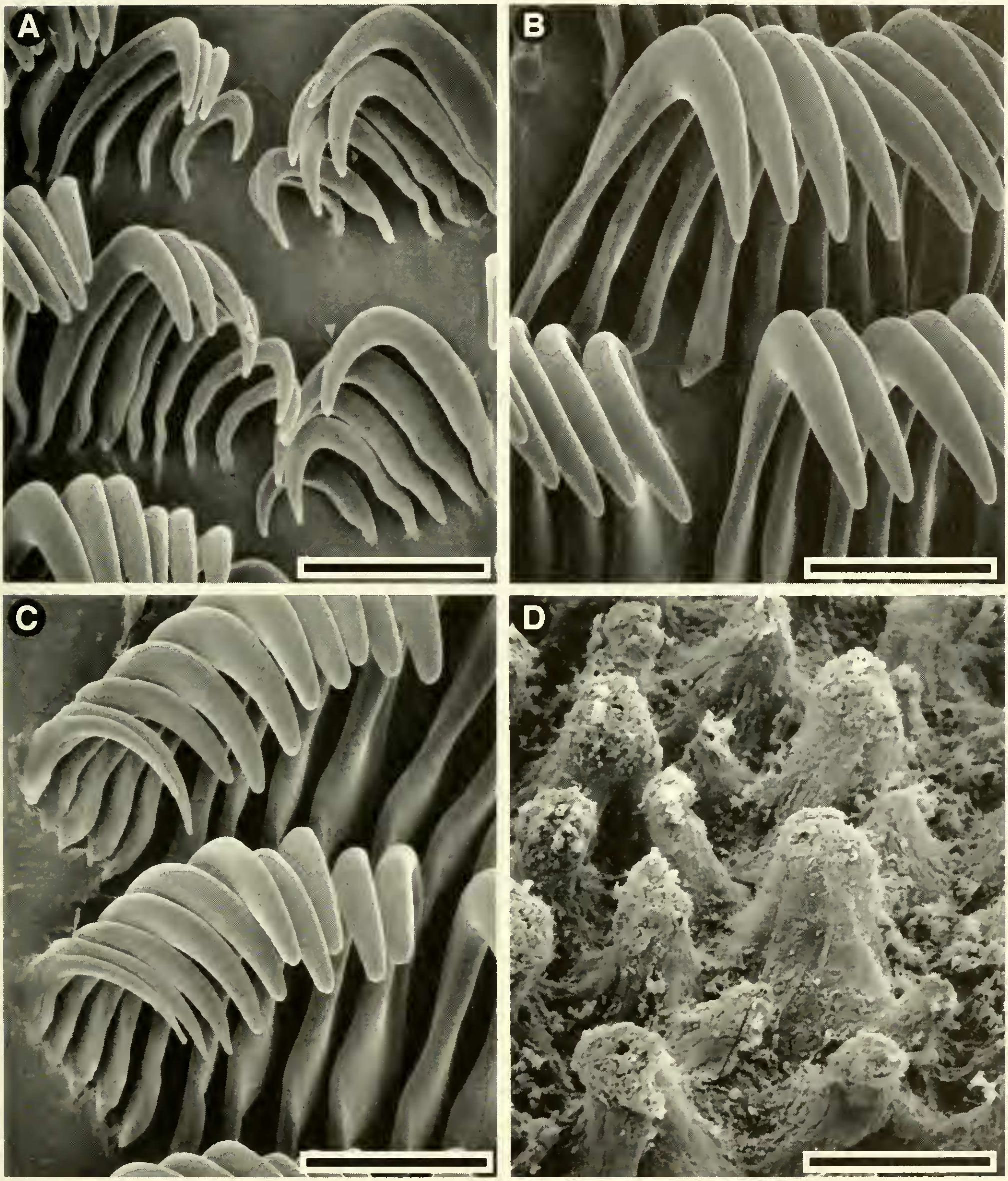

FIG. 30. *Peltodoris lippa,* new species, holotype. A. Inner lateral teeth; scale bar = 60 µm. B. Mid-lateral teeth; scale bar = 60 µm. C. Outer lateral teeth; scale bar = 60 µm. D. Dorsal tubercles; scale bar = 150 µm.

the cerebral and pleural ganglia are fused and distinct from the pedal ganglia. There are three cerebral nerves leading from each cerebral ganglion, and four pleural nerves lead from each pleural ganglion. The eyes are very large and inflated. The buccal ganglia lie near the rest of the central nervous system, joined to the cerebral ganglia by two short nerves. Gastroesophageal, rhinophoral, and optical ganglia are present. The pedal ganglia are clearly separated, with three (left side) and four (right side) nerves leading from them. The pedal and parapedal commissures are enveloped together with the visceral loop along all their length. There is an abdominal ganglion on the right side of the visceral loop.

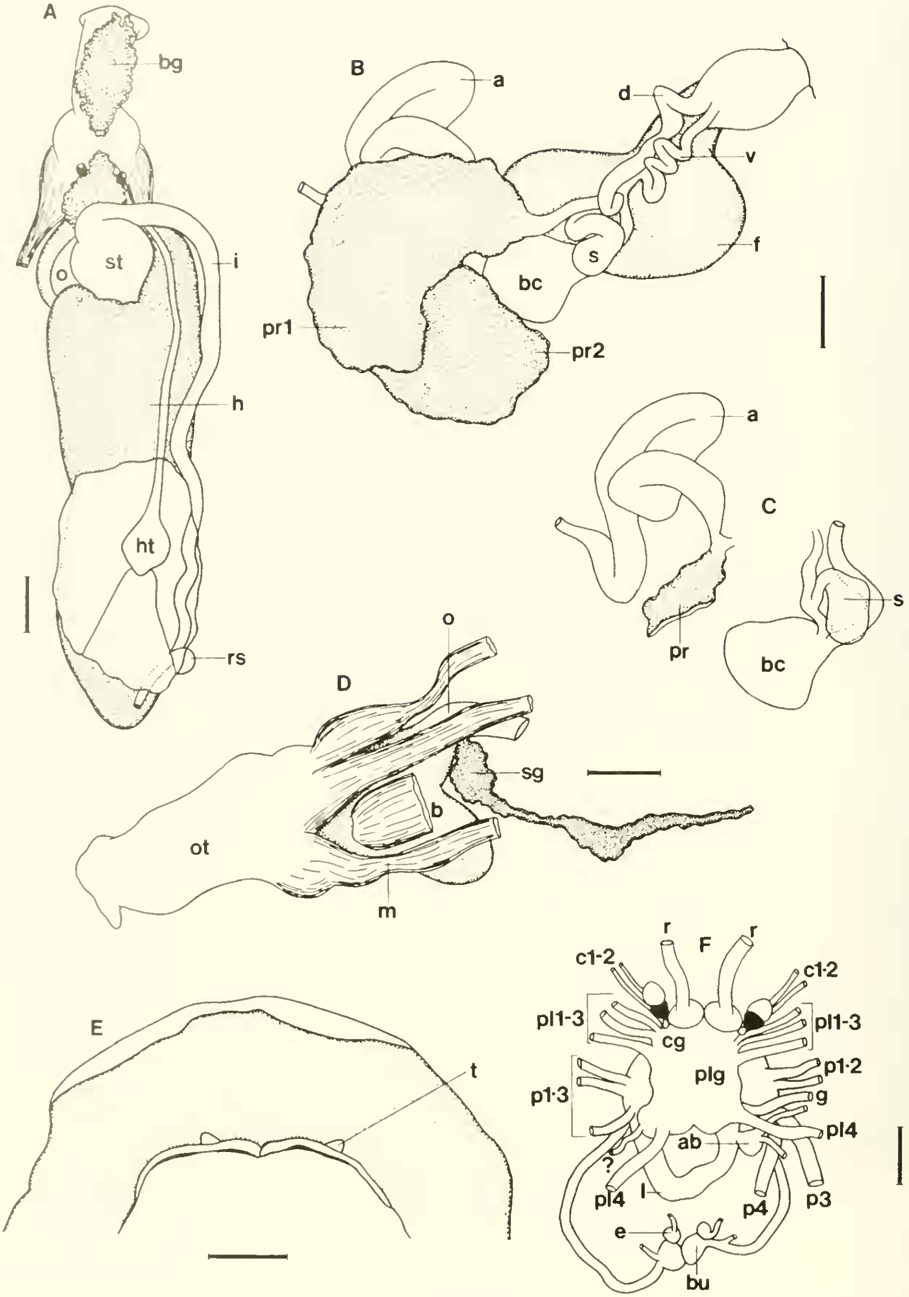

FIG. 31. *Peltodoris lippa,* new species, holotype. A. Dorsal view of the anatomy; scale bar = 1 mm. B. Reproductive system; scale bar = 0.5 mm. C. Detail of several reproductive organs; scale bar = 0.5 mm. D. Anterior portion of the digestive system; scale bar = 0.5 mm. E. Mouth area; scale bar = 1 mm. F. Central nervous system; scale bar = 0.5 mm. Abbreviations: a, ampulla; b, buccal bulb; ab, abdominal ganglion; bc, bursa copulatrix; bg, blood gland; bu, buccal ganglion; c, cerebral nerve; cg, cerebral ganglion; d, deferent duct; e, esophageal ganglion; f, female glands; g, genital nerve; h, hermaphrodite and digestive glands; ht, heart; i, intestine; l, visceral loop; m, retractor muscle; o, esophagus; ot, oral tube; p, pedal nerve; pl, pleural nerve; plg, pleural ganglion; pr, prostate; r, rhinophoral nerve; rs, renal syrinx; s, seminal receptacle; sg, salivary gland; st, stomach; t, oral tentacle; v, vagina.

The circulatory system (Fig. 31A) consists of a heart and two blood glands situated in front and behind the central nervous system.

Etymology

From the Latin *lippus* (having inflamed eyes), in reference to the large size of the eyeballs of this species.

Remarks

Peltodoris was regarded as a synonym of *Discodoris* by Thompson (1975), without any justification. Examination of specimens of *Peltodoris atromaculata* Bergh, 1880, the type species of the genus *Peltodoris*, revealed that this genus is distinguishable from *Discodoris* by the absence of jaw elements (Schmekel & Portmann, 1982). However, it is probable that the sole presence of this character, which is variable in other related genera, is not sufficient to separate *Peltodoris* from *Discodoris*. On the other hand, there may be other differences between these two genera that need to be investigated. A review of the systematic status and a reconstruction of the phylogeny of the cryptobranch dorids is necessary before definitive synonymies may be stabilized. In the meantime, the genus *Peltodoris* is here regarded as valid and different from *Discodoris*.

Peltodoris lippa shares a number of features with *Peltodoris atromaculata* Bergh, 1880, and it clearly belongs to this genus. These features in common are dorsum with simple, non-caryophyllidia tubercles, anterior border of the foot grooved and notched, oral tentacles present, radular teeth and labial cuticle smooth, absence of penial hooks or accessory glands, and flattened prostate.

This is the first species of *Peltodoris* described from deep waters, and it is clearly distinguishable from other species of the genus in having a uniform translucent white coloration.

The species of *Peltodoris* with the most proximal geographic range to *P. lippa* is *P. noumeae* (Risbec, 1937) described from shallow waters of New Caledonia. There is not enough information in the original description of this species (Risbec, 1937) to determine whether it belongs to the genus *Peltodoris*. In any case, *P. noumeae* is clearly distinguishable from *P. lippa* in having a yellow-orange background color with red spots.

Peltodoris fellowsi Kay & Young, 1969, originally described from Hawaii and subsequently reported from the Pitcairn Islands (Edmunds & Preece, 1996), has a uniform white coloration as well. However, in *P. fellowsi* the gill is black and the rhinophores are red-brown, whereas in *P. lippa* rhinophores and gill are white. Internally both species differ in the radular morphology. The outermost lateral teeth of *P. fellowsi* are shorter than those of *P. lippa*.

Genus *Paradoris* Bergh, 1884

Type Species: *Paradoris granulata* Bergh, 1884, by monotypy [= *Paradoris indecora* (Bergh, 1881)].

Paradoris araneosa Valdés, new species
(Figs. 13B, 32, 33)

Material Examined

HOLOTYPE: South of New Caledonia, Bathus 2 Expedition, stn. CP736 (23°03′S, 166°59′E), 452–464 m, 13 May 1993, 14 mm preserved length, leg. P. Bouchet and B. Richer de Forges (MNHN).

PARATYPES: South of New Caledonia, SMIB 8 Expedition, stn. DW182–184 (23°18′S–23°19′S, 168°05′E), 314–367 m, 31 January 1993, one specimen 35 mm preserved length, dissected, leg. P. Bouchet and B. Richer de Forges (MNHN). Norfolk Ridge, New Caledonia, Bathus 3 Expedition, stn. DW838 (23°01′S, 166°56′E), 400–402 m, 30 November 1993, one specimen 33 mm preserved length, dissected, leg. P. Bouchet, B. Richer de Forges and A. Warén (MNHN). Southeast of New Caledonia, Halipro 1 Expedition, stn. CP851 (21°43′S, 166°37′E), 314–364 m, 19 March 1994, one specimen 13 mm preserved length, dissected, leg. B. Richer de Forges (CASIZ 121099).

External Morphology

The body is elevated and oval (Fig. 13B). The dorsum is covered with simple, rounded tubercles. The dorsal surface, in the areas without tubercles, has a number of small depressions surrounded by minute ridges (Fig. 32E). The perfoliate rhinophores are composed of 25 lamellae. There are six tripinnate branchial leaves. Ventrally, the oral tentacles

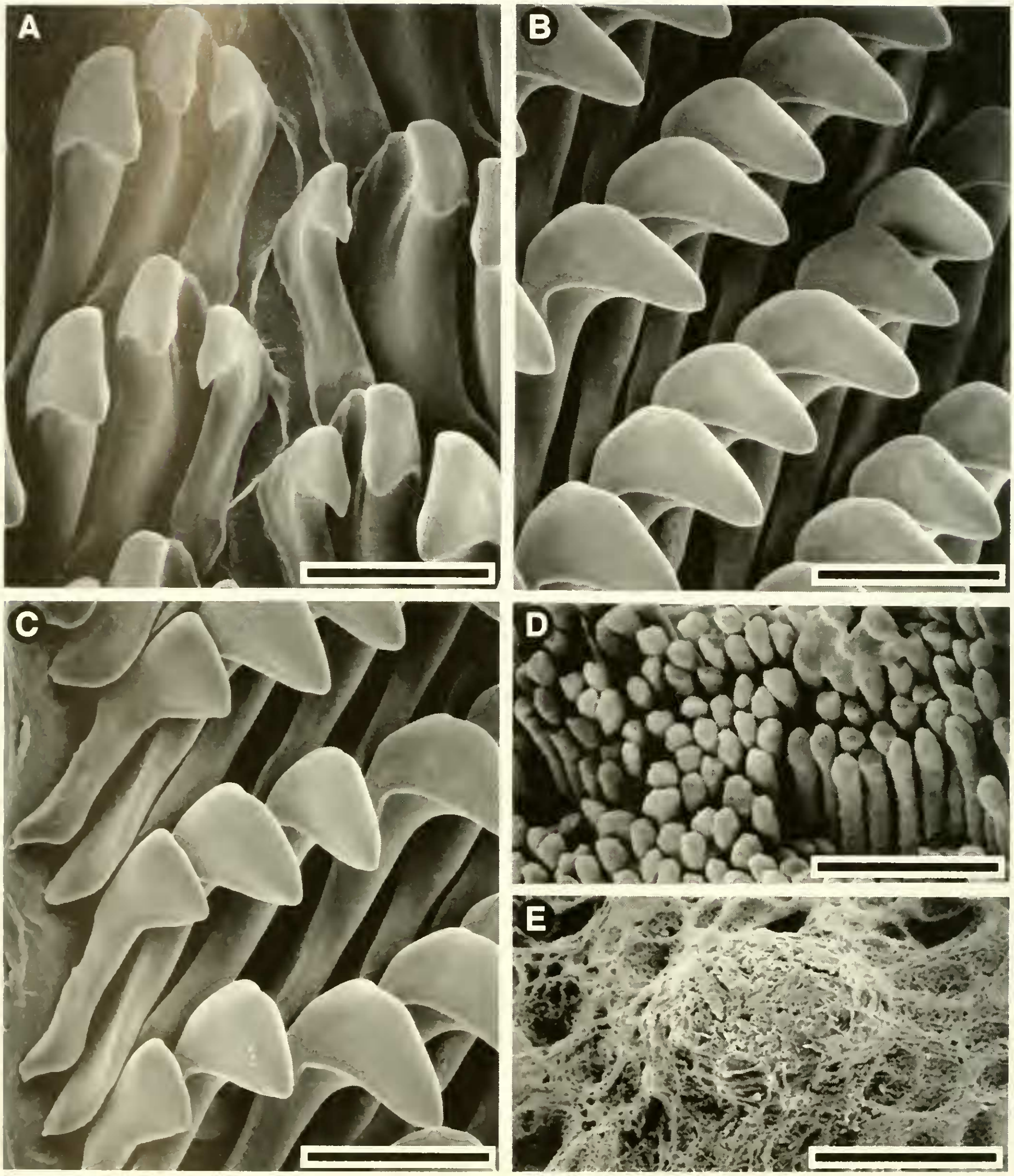

FIG. 32. *Paradoris araneosa*, new species, paratype from Bathus 3 (stn. DW838). A. Inner lateral teeth; scale bar = 75 µm. B. Mid-lateral teeth; scale bar = 100 µm. C. Outer lateral teeth; scale bar = 100 µm. D. Jaw elements; scale bar = 43 µm. E. Dorsal tubercles; scale bar = 600 µm.

are short and conical. The anterior border of the foot is notched and grooved (Fig. 33F). The mantle margin is about as wide as the foot.

Based on the photographs, the color of the living animals is pale brown. There are few, large, dark brown spots scattered on the dorsal surface and several, more numerous, small darker dots. The larger tubercles are opaque white. The rhinophores are cream with opaque white lamellae. The branchial leaves are pale brown and the lamellae dark

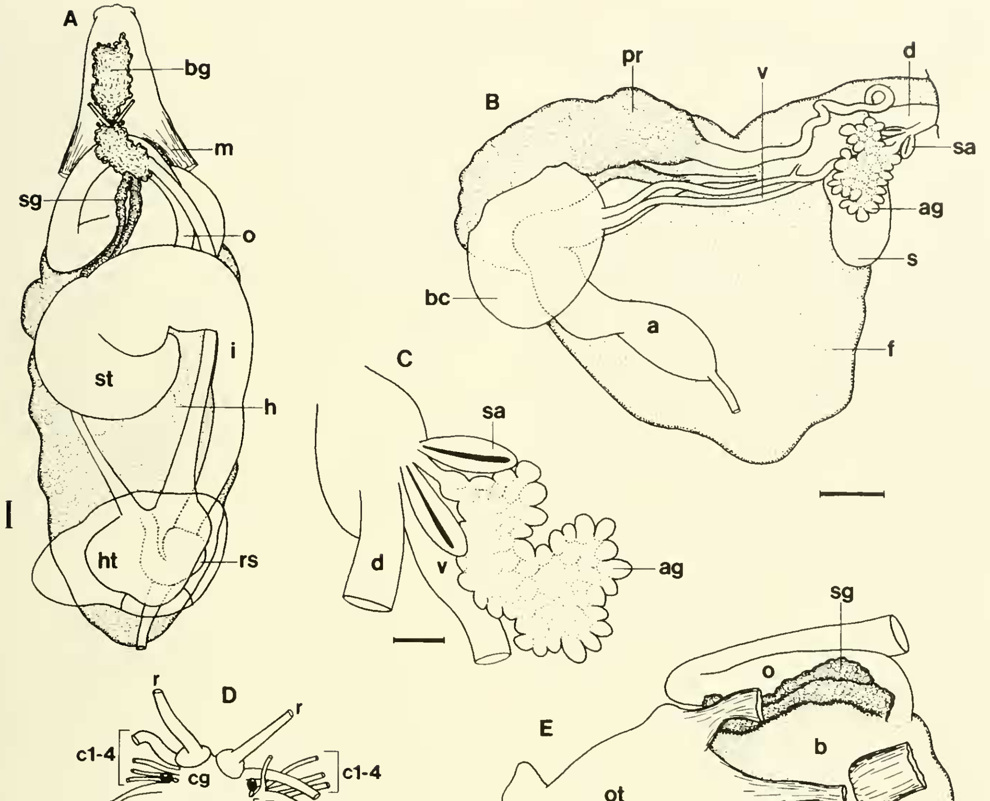

FIG. 33. *Paradoris araneosa*, new species, paratype from SMIB 8 (stn. DW182–184). A. Dorsal view of the anatomy; scale bar = 1 mm. B. Reproductive system; scale bar = 1 mm. C. Detail of the accessory organs; scale bar = 0.5 mm. D. Central nervous system; scale bar = 0.5 mm. E. Anterior portion of the digestive system; scale bar = 1 mm. F. Mouth area; scale bar = 1 mm. Abbreviations: a, ampulla; ag, accessory gland; b, buccal bulb; bc, bursa copulatrix; bg, blood gland; bu, buccal ganglion; c, cerebral nerve; cg, cerebral ganglion; d, deferent duct; e, esophageal ganglion; f, female glands; g, genital nerve; h, hermaphrodite and digestive glands; ht, heart; i, intestine; l, visceral loop; m, retractor muscle; o, esophagus; ot, oral tube; p, pedal nerve; pg, pedal ganglion; pl, pleural nerve; pr, prostate; r, rhinophoral nerve; rs, renal syrinx; s, seminal receptacle; sa, accessory sac; sg, salivary gland; st, stomach; t, oral tentacle; v, vagina.

brown. There are several white dots on the gill, more densely arranged near the base of the branchial leaves.

Anatomy

The posterior end of the oral tube has six strong retractor muscles (Fig. 33E), which are attached to the body wall. The oval, muscular buccal bulb has two additional muscles. The buccal bulb is about as long as the oral tube. The jaws consist of numerous thin, unicuspid elements about 30 μm long (Fig. 32D). The radular formula is 68 × (16.0.16) in a 32 mm preserved length specimen. There are no rachidian teeth. The inner lateral teeth are hamate, having a single cusp, and they lack denticles (Fig. 32A). The teeth are very elongate with a short, strong cusp. The teeth increase in size gradually towards the medial portion of the half-row (Figs. 32A, B). The outermost teeth are elongate and also lack denticles (Fig. 32C). The esophagus is long and connects directly to the stomach.

The ampulla is long and curved. It narrows into the gonoduct, which branches into a long oviduct and the prostate (Fig. 33B). The oviduct enters the female glands near the nidamental opening. The prostate is flattened and granular; it is divided into two portions that are clearly distinguishable by their different texture and coloration, the largest portion being pale yellow and connecting to the deferent duct, whereas the smallest portion is orange and connects to the ampulla. The deferent duct is long and narrow; it narrows and expands again into the short ejaculatory portion. The deferent duct opens into a common atrium with the vagina. The penis is unarmed. There is a large, ramified accessory gland and two small sacs, containing one rigid spine each, connected to the atrium (Fig. 33C). The vagina is very long; at its proximal end, it connects to the large and oval bursa copulatrix. From the bursa copulatrix leads another long duct that connects to the seminal receptacle and the very short uterine duct. The bursa copulatrix is about six times larger than the seminal receptacle.

In the central nervous system (Fig. 33D), the cerebral and pleural ganglia are fused and distinct from the pedal ganglia. There are four cerebral nerves leading from each cerebral ganglion, and four pleural nerves lead from each pleural ganglion. The buccal ganglia lie near the rest of the central nervous system, joined to the cerebral ganglia by two long nerves. Gastroesophageal, rhinophoral, and optical ganglia are present. The pedal ganglia are clearly separated, with three nerves leading from each. The pedal and parapedal commissures are enveloped together with the visceral loop along all their length.

The circulatory system (Fig. 33A) consists of a heart and two blood glands situated in front and behind the central nervous system.

Etymology

From the Latin *araneosus* (full of webs), in reference to the small ridges on the surface of this species, that resemble cobwebs.

Remarks

Paradoris araneosa belongs to the genus *Paradoris* in having the following combination of characters: anterior border of the foot notched and grooved, simple dorsal tubercles, reproductive system with an accessory gland and two rigid copulatory spines, jaws with numerous, simple elements, radula with strong teeth, which have a short cusp and lack denticles (Miller, 1995).

Paradoris leuca Miller, 1995, from New Zealand, is the species that has been found in closest proximity to *P. araneosa*. It differs from *P. araneosa* in lacking accessory glands and copulatory sacs armed with spines (Miller, 1995). Due to the lack of these structures, it is likely that *P. leuca* does not belong to the genus *Paradoris*. Other differences are the shape of the jaw elements, which have a triangular cusp in *P. leuca* and are rounded in *P. araneosa*. Externally, the dorsal tubercles of *P. leuca* are more evenly distributed and are smaller than those of *P. araneosa*.

Paradoris tsurugensis Baba, 1986, from Japan, is distinguishable from *P. araneosa* in having two accessory glands and two copulatory sacs armed with spines, instead of a single accessory gland (Baba, 1986). Also, *P. tsurugensis* has many more radular teeth than *P. araneosa* at comparable size. The radular formula of the former is 90 × (20-25.0.20-25), whereas it is 68 × (16.0.16) in the latter.

Miller (1995) included *Platydoris galbanus* Burn, 1958, from Victoria, Australia, and *Peltodoris fellowsi* Kay & Young, 1969, from Hawaii, in the genus *Paradoris*, but both species lack jaws (Burn, 1958; Kay & Young, 1969), and therefore they must be placed in a different genus.

Paradoris imperfecta Valdés, new species (Figs. 13C, 34, 35)

Material Examined

HOLOTYPE: South of New Caledonia, Chalcal 2 Expedition, stn. CP18 (24°47′S, 168°09′E), 274 m, 27 October 1986, 13 mm preserved length, leg. P. Bouchet, B. Métivier and B. Richer de Forges (MNHN).

External Morphology

The body is elevated and oval (Fig. 13C). The dorsum is covered with small, conical tubercles. There are several larger tubercles surrounded by smaller tubercles. Many tubercles, especially those situated in the center of the body, are joined to the adjacent ones by short ridges. The perfoliate rhinophores are composed of 20 lamellae. There are five bipinnate branchial leaves. Ventrally, the oral tentacles are short and conical. The anterior border of the foot is notched and grooved (Fig. 34F). The mantle margin is about as wide as the foot.

The color of the living animals is uniformly cream. There are few, irregular pale brown spots and numerous small dark brown dots on the dorsal surface. The dark brown spots are situated on the mantle margin. There are two areas on both sides of the dorsal hump with a high concentration of dark brown spots. The rhinophores are cream with the lamellae dark brown. The gill is uniformly cream.

Anatomy

The posterior end of the oral tube has six strong retractor muscles (Fig. 34E), which are attached to the body wall. The oval, muscular buccal bulb has two additional muscles. The buccal bulb is about as long as the oral tube. The jaws consist of numerous thin, unicuspid elements, about 10 μm long (Fig. 35C). The radular formula is 46 × (13.0.13) in a 13 mm preserved length specimen. There are no rachidian teeth. The inner lateral teeth are hamate, having a single cusp, and they lack denticles (Fig. 35A). The teeth are very elongate, with a short, strong cusp. The teeth increase in size gradually towards the medial portion of the half-row (Figs 35A–B). The outermost teeth are short and also lack denticles (Fig. 35C). The esophagus is long and connects directly to the stomach.

The ampulla is short and simple; it narrows into the gonoduct, which branches into the oviduct and the prostate (Fig. 34B). The oviduct enters the female glands near the nidamental opening. The prostate is long and granular; it is divided into two portions that are clearly distinguishable by their different texture and coloration. The larger portion is pale yellow and connects to the deferent duct, whereas the smaller portion is orange and connects to the ampulla. The deferent duct is short and narrow; it expands again into the long ejaculatory portion. The deferent duct opens into a common atrium with the vagina. The penis is unarmed. There are two small sacs connected to the atrium, each containing a single rigid spine each. The vagina is very long; at its proximal end, it connects to the large, oval bursa copulatrix. From the bursa copulatrix leads another long duct that connects to the irregular seminal receptacle and the uterine duct (Fig 34C). The bursa copulatrix is about five times larger than the seminal receptacle.

In the central nervous system (Fig. 34D), the cerebral and pleural ganglia are fused and distinct from the pedal ganglia. There are four cerebral nerves leading from each cerebral ganglion, and two pleural nerves lead from each pleural ganglion. The buccal ganglia lie near the rest of the central nervous system, joined to the cerebral ganglia by two long nerves. Gastroesophageal, rhinophoral, and optical ganglia are present. The pedal ganglia are clearly separated, having two nerves leading from each one. The pedal and parapedal commissures are enveloped together with the visceral loop along all their length.

The circulatory system (Fig. 34A) consists of a heart and two blood glands situated in front and behind the central nervous system.

Etymology

From the Latin *imperfectus* (imperfect), in reference to the lack of accessory gland in this species and the irregular shape of the seminal receptacle.

Remarks

Paradoris imperfecta is clearly distinguishable from *P. araneosa* in lacking an accessory

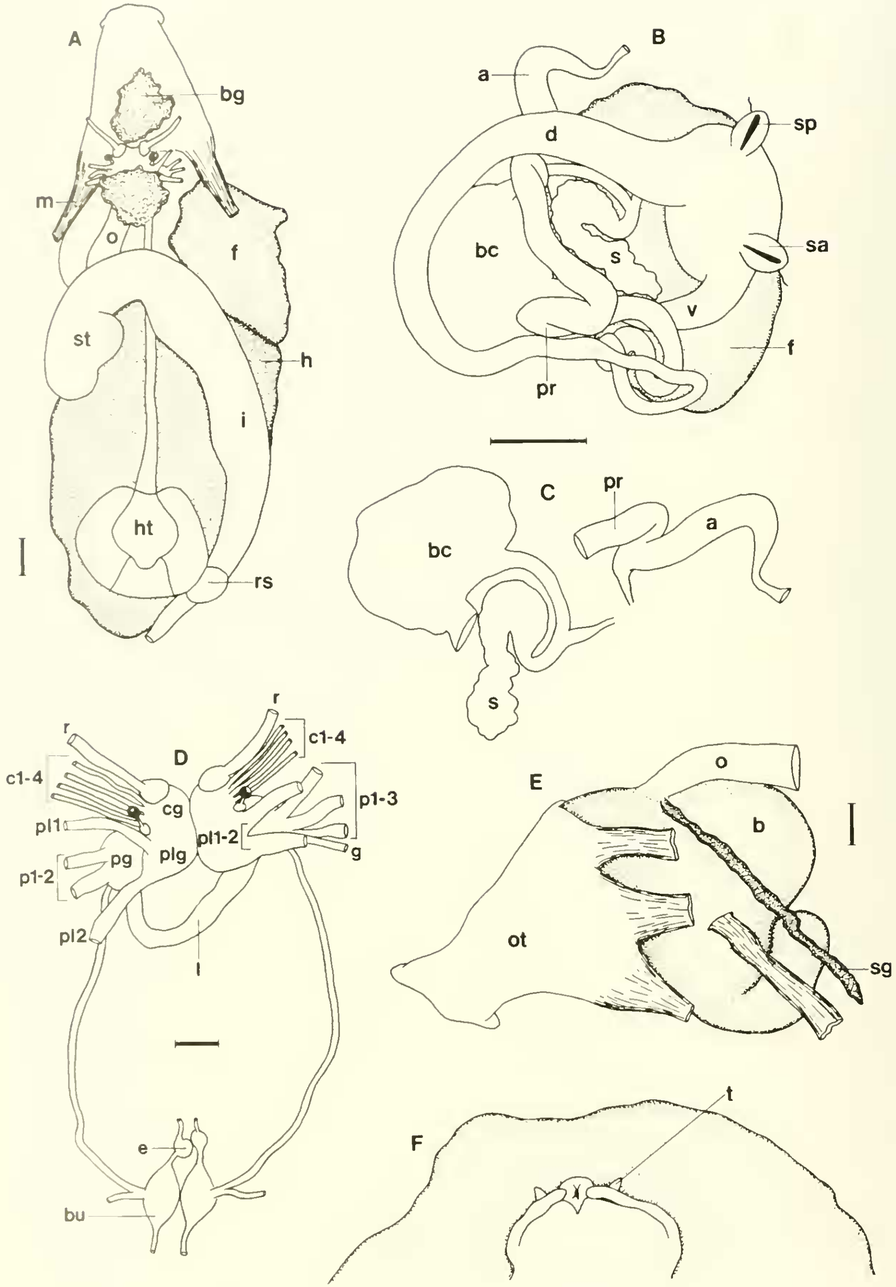

FIG. 34. *Paradoris imperfecta,* new species, holotype. A. Dorsal view of the anatomy; scale bar = 1 mm. B. Reproductive system; scale bar = 1 mm. C. Detail of several reproductive organs; scale bar = 1 mm. D. Central nervous system; scale bar = 0.5 mm. E. Anterior portion of the digestive system; scale bar = 0.5 mm. F. Mouth area; scale bar = 1 mm. Abbreviations: a, ampulla; b, buccal bulb; bc, bursa copulatrix; bg, blood gland; bu, buccal ganglion; c, cerebral nerve; cg, cerebral ganglion; d, deferent duct; e, esophageal ganglion; f, female glands; g, genital nerve; h, hermaphrodite and digestive glands; ht, heart; i, intestine; l, visceral loop; m, retractor muscle; o, esophagus; ot, oral tube; p, pedal nerve; pg, pedal ganglion; pl, pleural nerve; plg, pleural ganglion; pr, prostate; r, rhinophoral nerve; rs, renal syrinx; s, seminal receptacle; sa, accessory sac; sg, salivary gland; sp, accessory spine; st, stomach; t, oral tentacle; v, vagina.

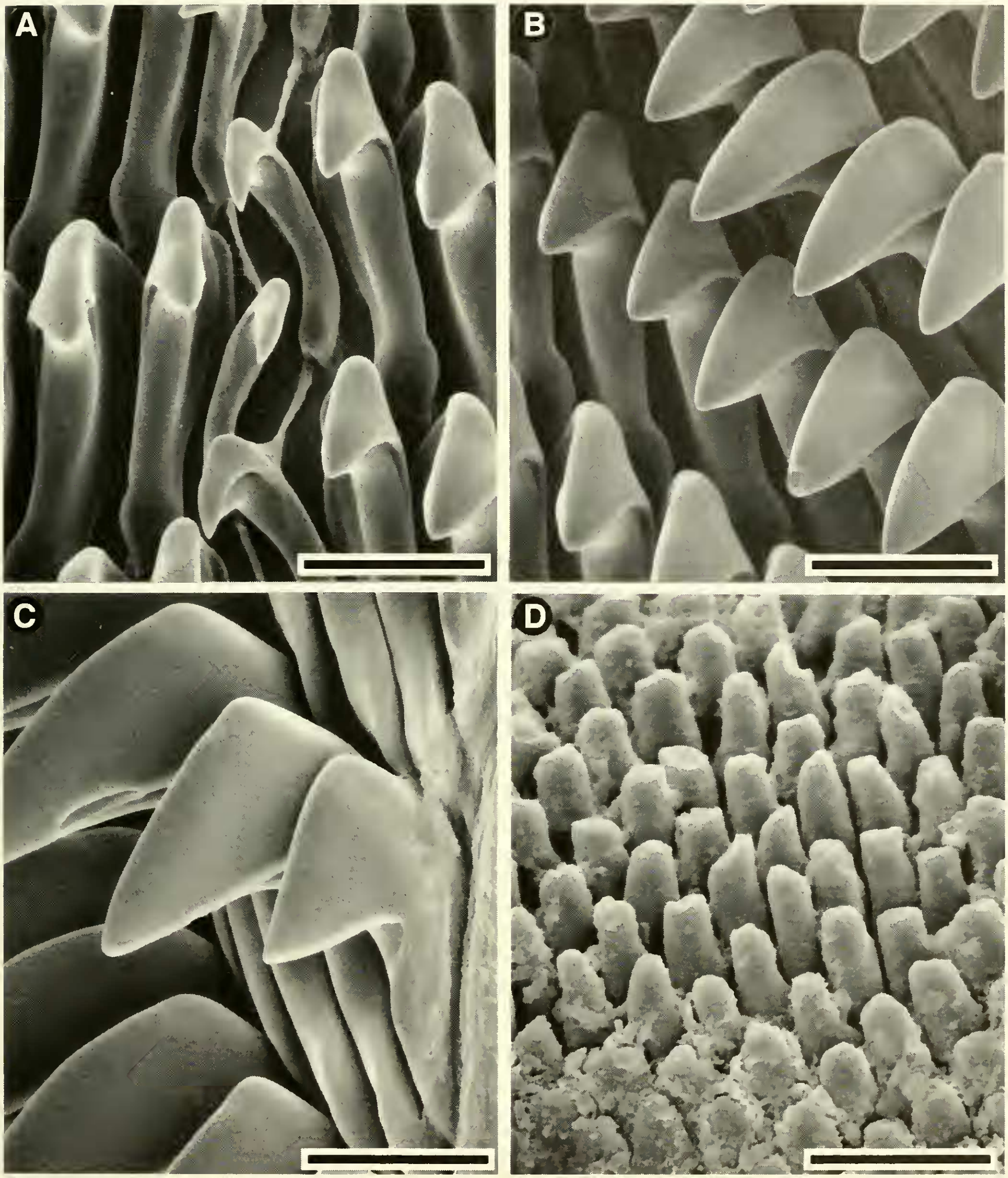

FIG. 35. *Paradoris imperfecta,* new species, holotype. A. Inner lateral teeth; scale bar = 43 µm. B. Mid-lateral teeth; scale bar = 43 µm. C. Outer lateral teeth; scale bar = 30 µm. D. Jaw elements; scale bar = 20 µm.

gland. In addition, *P. imperfecta* has only two accessory sacs containing spines, which also distinguish this species from *Paradoris leuca* and *P. tsurugensis. Paradoris leuca* does not have accessory glands or sacs, whereas *P. tsurugensis* has two glands and two sacs.

Anatomical differences between *P. araneosa* and *P. imperfecta* include the outermost lateral teeth of the radula, which are much shorter in *P. imperfecta*. Also, the lateral teeth appear to have a longer, more triangular cusp in *P. imperfecta*. The prostate of *P. imperfecta* is more elongate than that of *P. araneosa,* and the seminal receptacle is irregular and elongate, whereas in *P. araneosa* it is regularly oval. Also, the atrium of *P. imperfecta* is much larger and the vagina is shorter than those of *P. araneosa*.

Externally, these two species differ in the coloration of the rhinophores and the gill. The rhinophores of *P. araneosa* have white lamellae, whereas in *P. imperfecta* the lamellae are dark brown. The gill of *P. araneosa* is pale brown with dark brown lamellae and white dots, whereas it is uniformly cream in *P. imperfecta*.

Genus *Diaulula* Bergh, 1878

Type Species: *Doris sandiegensis* Cooper, 1863, by monotypy.

Diaulula immaculata Valdés, new species
(Figs. 29C, 36, 37)

Material Examined

HOLOTYPE: Loyalty Ridge, Musorstom 6 Expedition, stn. DW428 (20°24′S, 166°13′E), 420 m, 17 February 1989, 19 mm preserved length, leg. P. Bouchet and B. Richer de Forges (MNHN).

PARATYPE: Chesterfield, Coral Sea, Musorstom 5 Expedition, stn. 371 (19°55′S, 158°38′E), 350 m, 20 October 1986, one specimen 9 mm preserved length, leg. P. Bouchet, B. Métivier and B. Richer de Forges (MNHN).

External Morphology

The body is elevated and oval (Fig. 29C). The dorsum is covered with thin caryophyllidia, the largest reaching over 75 μm (Fig. 36D). They have a large, rounded ciliated tubercle and 6–7 spicules around it. The perfoliate rhinophores are composed of 20 lamellae. There are four bipinnate branchial leaves. Ventrally, the oral tentacles are short and conical. The anterior border of the foot is notched and grooved (Fig. 37E). The mantle margin is wider than the foot.

The color of the living animals is unknown. Preserved specimens are uniformly pale cream. The rhinophores and gill are also pale cream.

Anatomy

The posterior end of the oral tube has six strong retractor muscles (Fig. 37D), which are attached to the body wall. The oval, muscular buccal bulb has two additional muscles. The oral tube is about twice as long as the buccal bulb. The labial cuticle is smooth. The radular formula is 32 × (46.0.46) in a 9 mm preserved length specimen. There are no rachidian teeth. The inner lateral teeth are hamate, having a single cusp, and they lack denticles (Fig. 36A). The teeth are very elongate with a short, strong cusp. The teeth increase in size gradually towards the medial portion of the half-row (Figs. 36A, B). The outermost teeth are short and also lack denticles (Fig. 36C). The esophagus connects directly to the stomach.

The ampulla is long and convoluted; it narrows into the gonoduct, which branches into the oviduct and the prostate (Fig. 37C). The oviduct enters the female glands near the center of the mass. The prostate is very large and granular (Fig 37B); it is divided into two portions that are clearly distinguishable by their different texture and coloration; the largest portion is pale yellow and connects to the deferent duct, whereas the smallest portion is orange and connects to the ampulla. The deferent duct is long and narrow, and opens into a common atrium with the vagina. The penis is unarmed. The vagina is long; at its proximal end, it connects to the large, oval bursa copulatrix. From the bursa copulatrix leads another long duct that connects to the seminal receptacle and the uterine duct. The bursa copulatrix is about six times larger than the seminal receptacle.

The circulatory system (Fig. 37A) consists of a heart and two blood glands situated in front and behind the central nervous system.

Etymology

From the Latin *immaculatus* (unspotted), in reference to the uniformly white dorsum of this species.

Remarks

Valdés & Gosliner (in press) revised the type species of the genus *Diaulula* and proposed a new diagnosis of the genus that includes the following characteristics: dorsum covered with elongate caryophyllidia, prostate flattened, with two portions, penis and vagina unarmed, labial cuticle smooth and radular teeth hamate and smooth. *Diaulula immaculata* has all these features and clearly belongs to this genus.

Several species have been assigned to the

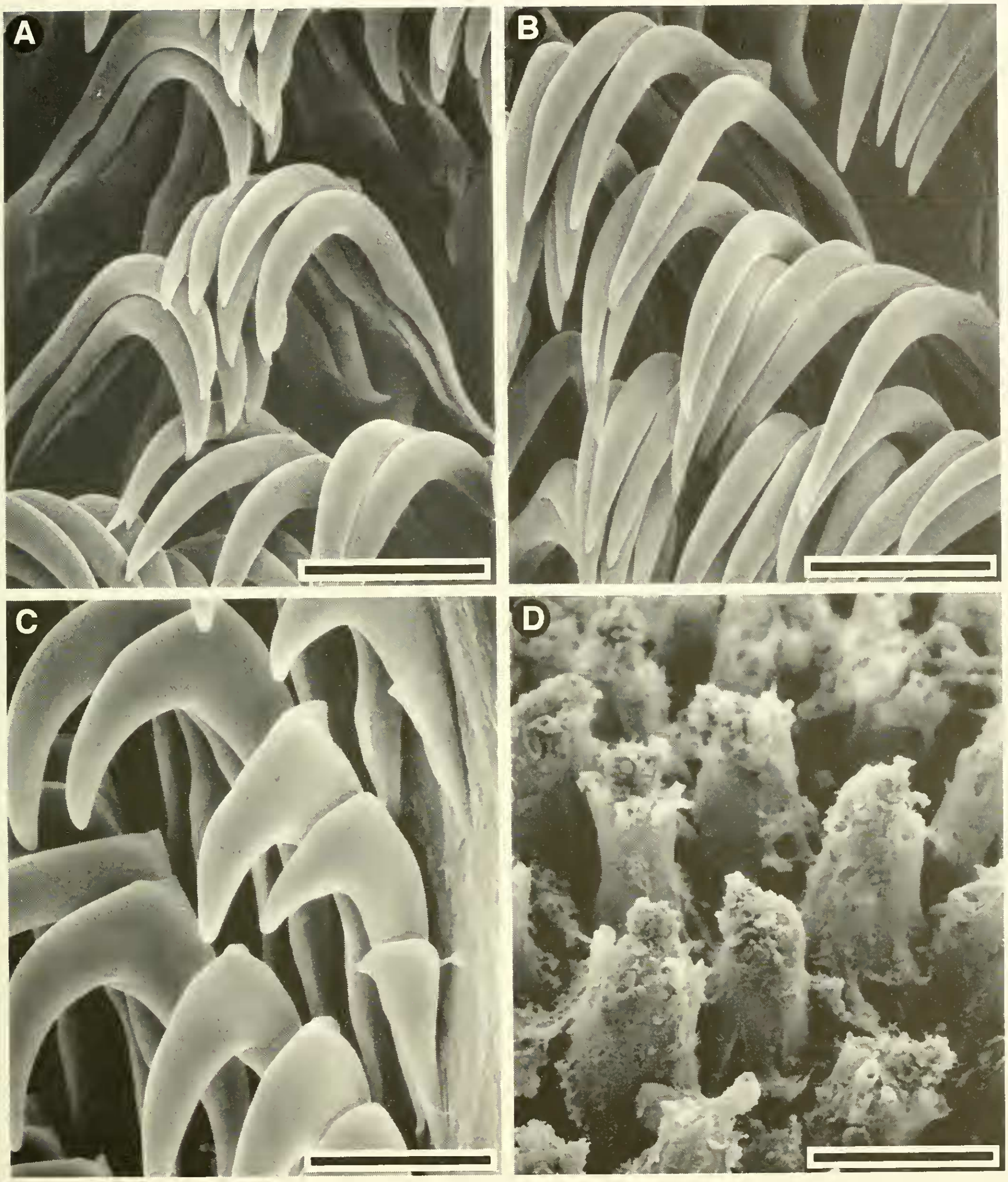

FIG. 36. *Diaulula immaculata,* new species, paratype. A. Inner lateral teeth; scale bar = 25 μm. B. Mid-lateral teeth; scale bar = 30 μm. C. Outer lateral teeth; scale bar = 20 μm. D. Caryophyllidia; scale bar = 75 μm.

genus *Diaulula* after its original description, which was based on *Doris sandiegensis* Cooper, 1863, from California. Bergh (1905) described *Diaulula rubra* from the Philippines, but the description is very incomplete and it is impossible to determine the correct generic placement of this species. Two years later, Bergh (1907) described two new species from South Africa, *D. capensis* and, with question, *D. morosa*. Both species appear to have caryophyllidia on the dorsum, but their reproductive systems are not described in enough detail to determine their correct generic placement. In any case, these species are distin-

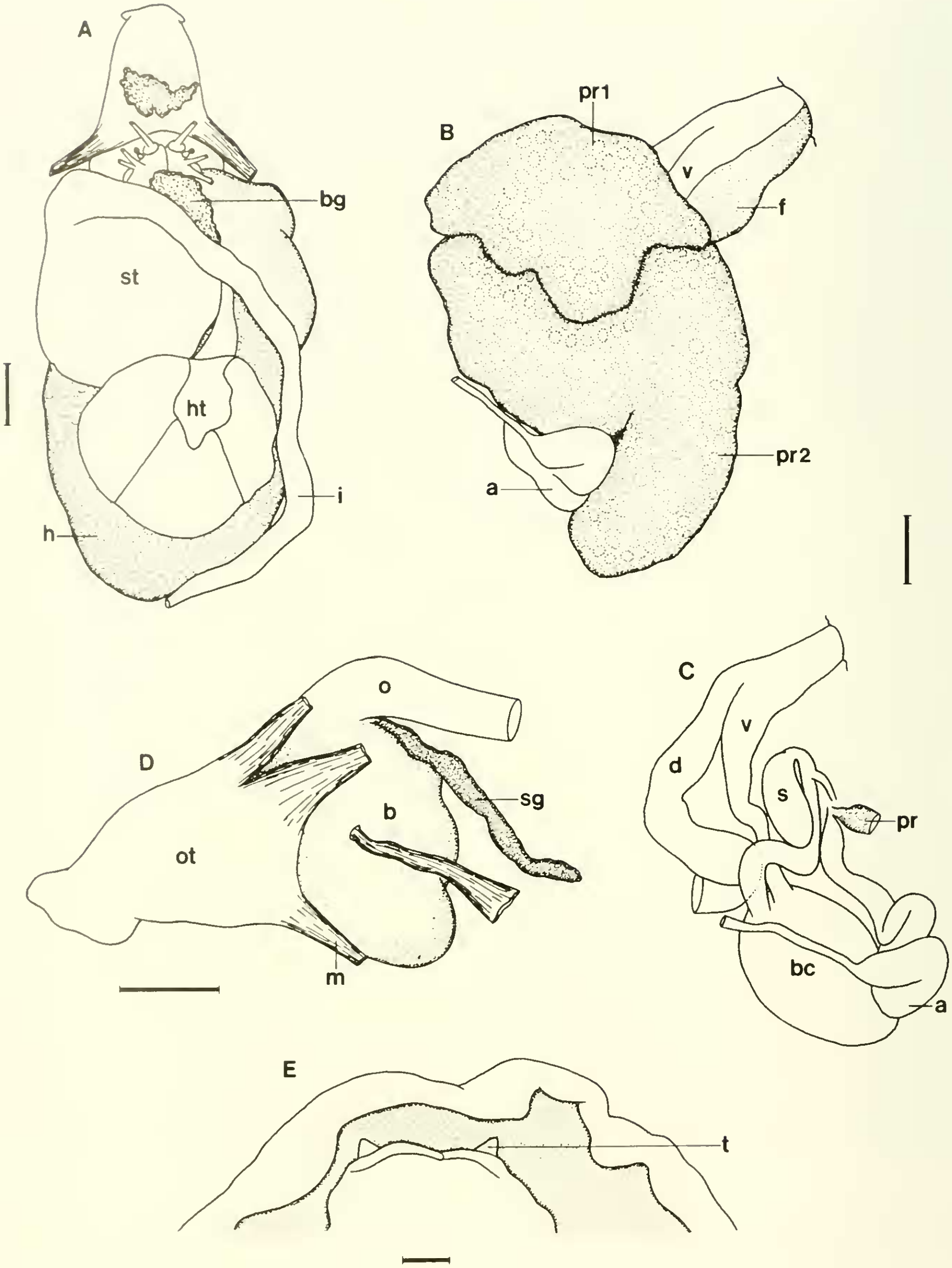

FIG. 37. *Diaulula immaculata*, new species, paratype. A. Dorsal view of the anatomy; scale bar = 1 mm. B. Reproductive system; scale bar = 0.5 mm. C. Detail of several reproductive organs; scale bar = 0.5 mm. D. Anterior portion of the digestive system; scale bar = 1 mm. E. Mouth area; scale bar = 0.5 mm. Abbreviations: a, ampulla; b, buccal bulb; bc, bursa copulatrix; bg, blood gland; d, deferent duct; f, female glands; h, hermaphrodite and digestive glands; ht, heart; i, intestine; m, retractor muscle; o, esophagus; ot, oral tube; pr, prostate; s, seminal receptacle; sg, salivary gland; st, stomach; t, oral tentacle; v, vagina.

guishable from *D. immaculata* by their external coloration, light brown in *D. capensis,* dark greenish in *D. morosa,* and uniformly white in *D. immaculata.*

Eliot (1907) transferred *Doris vestita* Abraham, 1877, to the genus *Diaulula.* Again, this species appears to have caryophyllidia, but the internal anatomy is not described in enough detail and its generic placement remains uncertain. Er. Marcus (1959) redescribed *Doris hispida* d'Orbigny, 1837, and placed this species in the genus *Diaulula.* This species has a dorsal ridge and could be a member of the genus *Atagema* J. E. Gray, 1850 (Valdés & Gosliner, in press).

Diaulula immaculata is clearly distinguishable from *D. sandiegensis* by both the external morphology and anatomy. Externally, *D. sandiegensis* has very distinctive black circles or spots on the dorsum that are absent in *D. immaculata.* Also, the outermost radular teeth of *D. sandiegensis* are more elongated and the prostate comparatively smaller than those of *D. immaculata.*

Diaulula cerebralis Valdés, new species
(Figs 29E, 38, 39)

Material Examined

HOLOTYPE: Philippines, Musorstom 3 Expedition, stn. CP144 (11°02′N, 124°15′E), 379–383 m, 7 June 1985, 30 mm preserved length, leg. P. Bouchet and M. P. Triclot (MNHN).

PARATYPE: Philippines, Musorstom 3 Expedition, stn. CP128 (11°50′N, 121°42′E), 815–321 m, 5 June 1985, one specimen 27 mm preserved length, dissected, leg. P. Bouchet and M. P. Triclot (MNHN).

External Morphology

The body is elevated and oval (Fig. 29E). The dorsum is covered with long, thin caryophyllidia, the largest reaching over 250 μm (Fig. 38E). They have a large, oval ciliated tubercle and four long spicules around it. The perfoliate rhinophores are composed of 30 lamellae. There are eight bipinnate branchial leaves. The rhinophoral and branchial sheaths are elevated. Ventrally, the oral tentacles are short and conical. The anterior border of the foot is notched and grooved (Fig. 39F). The mantle margin is about as wide as the foot.

The color of the living animals is uniformly white. The rhinophores and gill are also white.

Anatomy

The posterior end of the oral tube has six strong retractor muscles (Fig. 39E), which are attached to the body wall. The oval, muscular buccal bulb has two additional muscles. The buccal bulb is about as long as the thin oral tube. The jaws consist of numerous thin, unicuspid elements, about 10 μm long (Fig. 38D). The radular formula is 21 × (21.0.21) in a 27 mm preserved length specimen. There are no rachidian teeth. The three innermost lateral teeth are simple plates, lacking a cusp and denticles (Fig. 38A). The following lateral teeth have a single, short cusp and also lack denticles (Figs 38A–B). The teeth increase in size gradually towards the medial portion of the half-row. The outermost teeth are short, hamate and also lack denticles (Fig. 38C). The esophagus is long and connects directly to the stomach (Fig. 39A).

The ampulla is long and very convoluted; it narrows into the gonoduct, which branches into the short oviduct and the prostate (Fig. 39C). The oviduct enters the female glands near the nidamental opening. The prostate is long and granular (Fig. 39B); it narrows and expands again into the very large deferent duct, which opens into a common atrium with the vagina. The penis is unarmed. The vagina is wide and long; at its proximal end, it connects to the oval bursa copulatrix. From the distal end of the vagina leads another long duct that connects to the seminal receptacle and the uterine duct. The bursa copulatrix is about two times larger than the seminal receptacle.

In the central nervous system (Fig. 39D), the cerebral and pleural ganglia are partially fused and distinct from the pedal ganglia. The cerebral ganglia are very large and conspicuous. There are two cerebral nerves leading from each cerebral ganglion, and three (right side) or two (left side) pleural nerves lead from the pleural ganglion. The buccal ganglia lie near the rest of the central nervous system, joined to the cerebral ganglia by two long nerves. Gastroesophageal, rhinophoral and optical ganglia are present. The pedal ganglia are clearly separated, having three (right side) or four (left side) pedal nerves leading from them. The pedal and parapedal commissures are enveloped together with the visceral loop along all their length.

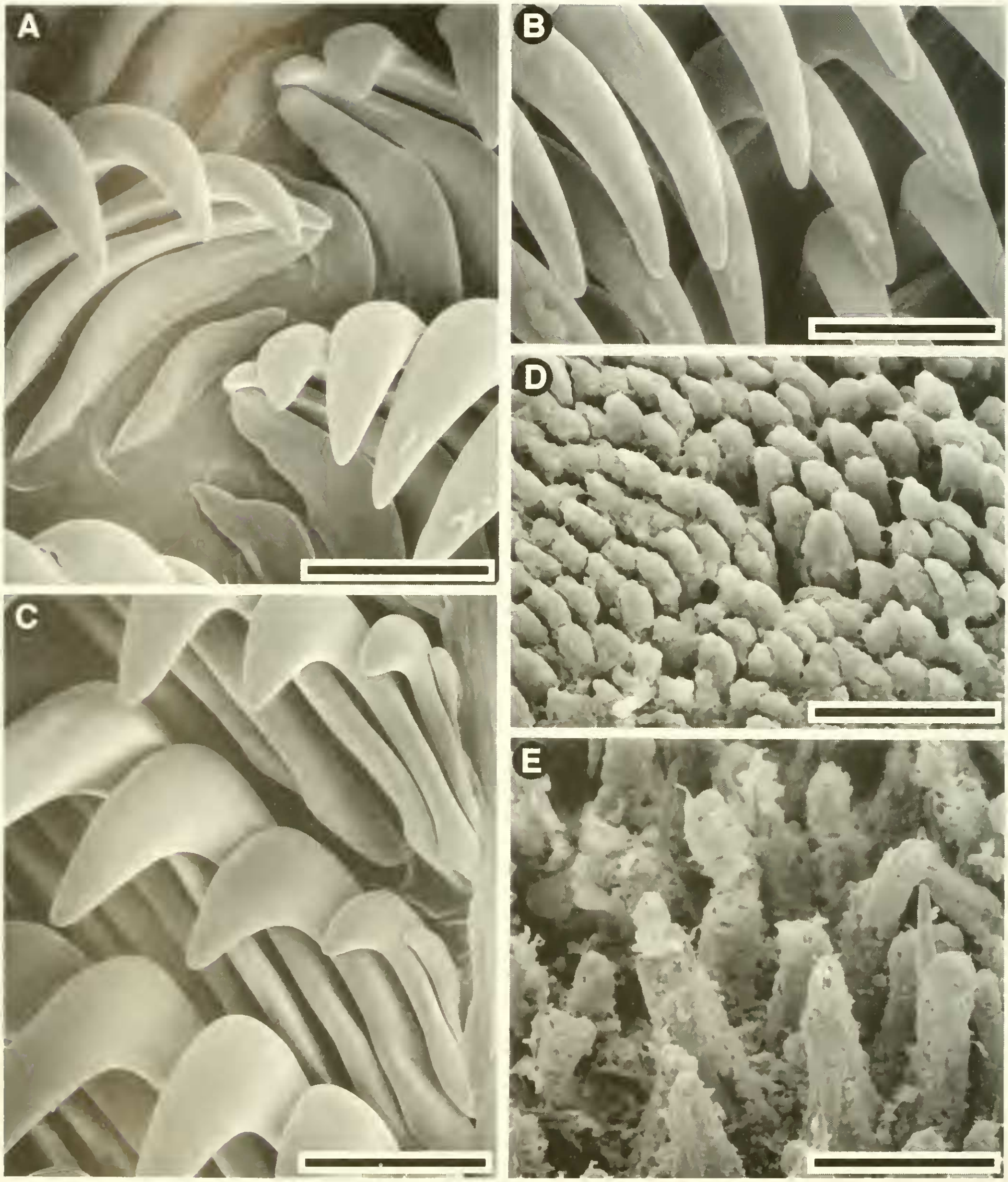

FIG. 38. *Diaulula cerebralis,* new species, paratype. A. Inner lateral teeth; scale bar = 100 μm. B. Mid-lateral teeth; scale bar = 100 μm. C. Outer lateral teeth; scale bar = 100 μm. D. Jaw elements; scale bar = 20 μm. E. Caryophyllidia; scale bar = 250 μm.

The circulatory system (Fig. 39A) consists of a heart and two blood glands situated in front and behind the central nervous system.

Etymology

From the Latin *cerebrum* (brain), in reference to the extremely developed cerebral ganglia of this species.

Remarks

The generic position of this species is particularly problematic. It fits within the genus *Diaulula* in having the dorsum covered with elongate caryophyllidia, prostate flattened, with two portions, penis and vagina unarmed and radular teeth hamate and smooth. However, it is different from the other species of

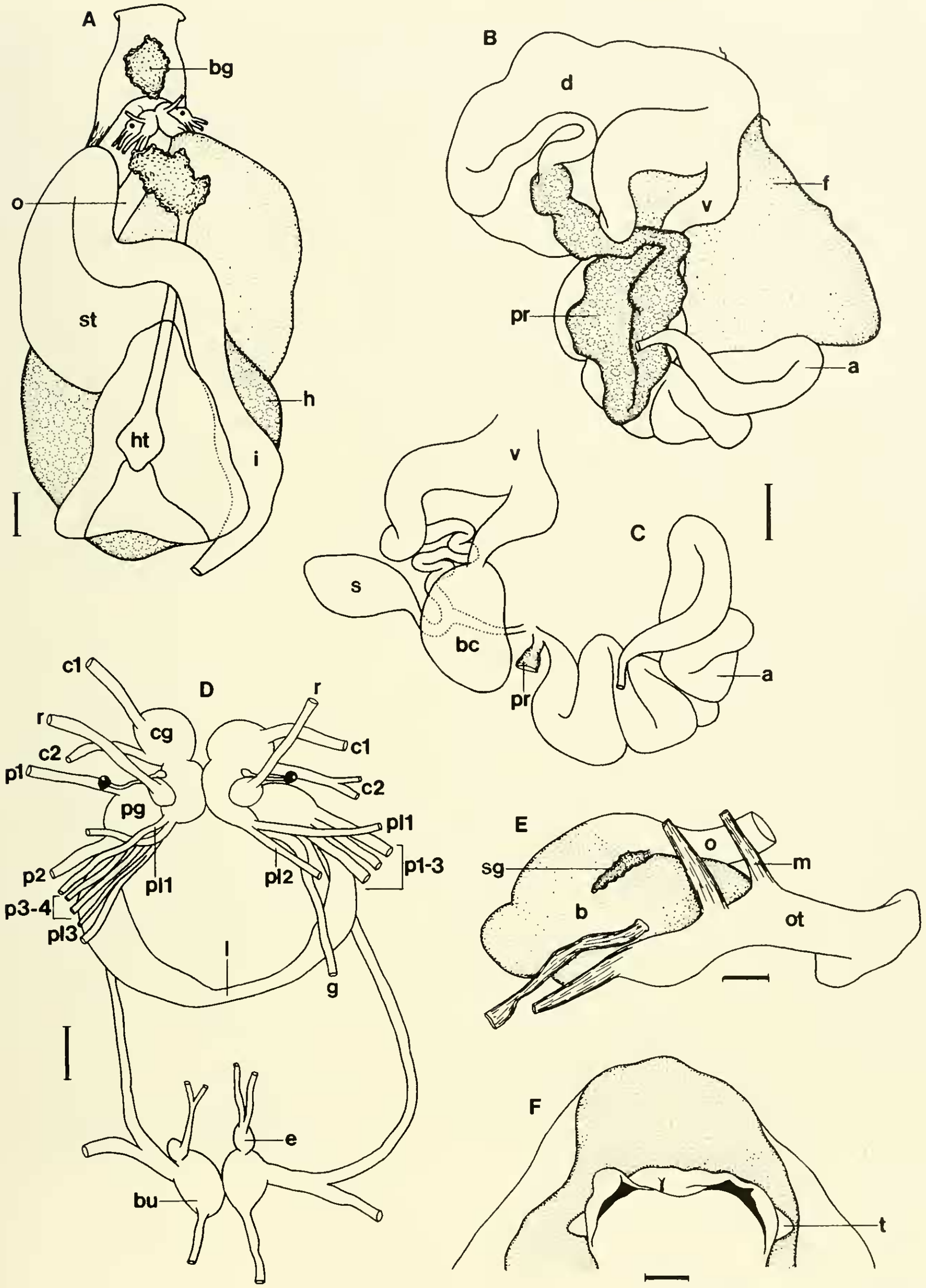

FIG. 39. *Diaulula cerebralis*, new species, paratype. A. Dorsal view of the anatomy; scale bar = 1 mm. B. Reproductive system; scale bar = 1 mm. C. Detail of several reproductive organs; scale bar = 1 mm. D. Central nervous system; scale bar = 0.5 mm. E. Anterior portion of the digestive system; scale bar = 0.5 mm. F. Mouth area; scale bar = 1 mm. Abbreviations: a, ampulla; b, buccal bulb; bc, bursa copulatrix; bg, blood gland; bu, buccal ganglion; c, cerebral nerve; cg, cerebral ganglion; d, deferent duct; e, esophageal ganglion; f, female glands; g, genital nerve; h, hermaphrodite and digestive glands; ht, heart; i, intestine; l, visceral loop; m, retractor muscle; o, esophagus; ot, oral tube; p, pedal nerve; pg, pedal ganglion; pl, pleural nerve; pr, prostate; r, rhinophoral nerve; s, seminal receptacle; sg, salivary gland; st, stomach; t, oral tentacle; v, vagina.

this genus in having jaws. The presence or absence of jaws is variable in other genera, such as *Rostanga* and *Jorunna,* and may not have much phylogenetic information (Valdés & Gosliner, in press). Other related genera in which this species could fit are *Rostanga* and *Jorunna*. However, *Rostanga* has very elongate and denticulate lateral teeth, and *Jorunna* has a large accessory gland with a copulatory spine. These characters are absent in *Diaulula cerebralis*. Therefore, this species is provisionally placed in the genus *Diaulula* where it is better accommodated.

Diaulula cerebralis differs from *D. immaculata* in having a much smaller prostate, the seminal receptacle connected to the vagina, instead of to the bursa copulatrix, the innermost lateral teeth like simple plates, and the cerebral ganglia extremely developed compared to other dorid central nervous systems previously studied (Valdés & Gosliner, in press). However, the most important difference between these two species is the presence of jaws in *Diaulula cerebralis*. *Diaulula sandiegensis* is also different from *D. cerebralis* in having dorsal black circles or spots and lacking jaws.

Genus *Rostanga* Bergh, 1879

Type Species: *Doris coccinea* Forbes, in Alder and Hancock, 1848, by original designation [= *Rostanga rubra* (Risso, 1818)].

Rostanga ankyra Valdés, new species

(Figs. 29B, 40, 41)

Material Examined

HOLOTYPE: South of New Caledonia, Chalcal 2 Expedition, stn. DW74 (24°40′S, 168°38′E), 650 m, 29 October 1985, 8 mm preserved length, leg. P. Bouchet, B. Métivier and B. Richer de Forges (MNHN).

External Morphology

The body is elevated and oval (Fig. 29B). The dorsum is covered with long, thin caryophyllidia, the largest reaching over 100 µm (Fig. 40D). They have a large ciliated tubercle and 5–6 spicules around it. The perfoliate rhinophores are composed of 19, transverse lamellae. There are five bipinnate branchial leaves. Ventrally, the oral tentacles are short and conical. The anterior border of the foot is notched and grooved. The mantle margin is about as wide as the foot.

The color of the living animal is uniformly white. The rhinophores and gill are also white.

Anatomy

The single specimen was poorly preserved and only the radula and reproductive system were examined. The labial cuticle is smooth. The radular formula is 77 × (97.0.97) in a 8 mm preserved length specimen. There are no rachidian teeth. The inner lateral teeth are hamate, having a long, thin cusp folded inwards, and a single, long denticle on the outer side (Fig. 40A). The base is very wide, triangular. The teeth increase in size gradually towards the medial portion of the half-row (Fig. 40A, B). The mid-lateral teeth are very long, with a curved cusp and two long denticles. The outermost teeth are also very elongate, with a single, long denticle (Fig. 40C).

The ampulla is short; it narrows into the gonoduct, which branches into a short oviduct and the prostate (Fig. 41). The oviduct enters the female glands near the center of the mass. The prostate is long and granular; it is divided into two portions that are clearly distinguishable by their different texture and coloration. The deferent duct is very long and narrow; it opens into a common atrium with the vagina. The vagina is very long; it expands into a large, muscular portion that narrows again before it connects to the large and irregular bursa copulatrix. From the bursa copulatrix leads another long duct that connects to the seminal receptacle and the short uterine duct. The bursa copulatrix is about twenty times larger than the seminal receptacle.

Etymology

From the Ancient Greek *ankyra* (anchor), in reference to the shape of the innermost radular teeth of this species.

Remarks

The radular morphology of *R. ankyra* is typical of the genus *Rostanga*. It is characterized by having the innermost teeth with a triangular, wide base and a cusp folded inwards, and the outermost teeth very elongate. Also, the oval body shape and the presence of long caryophyllidia on the dorsum clearly suggest

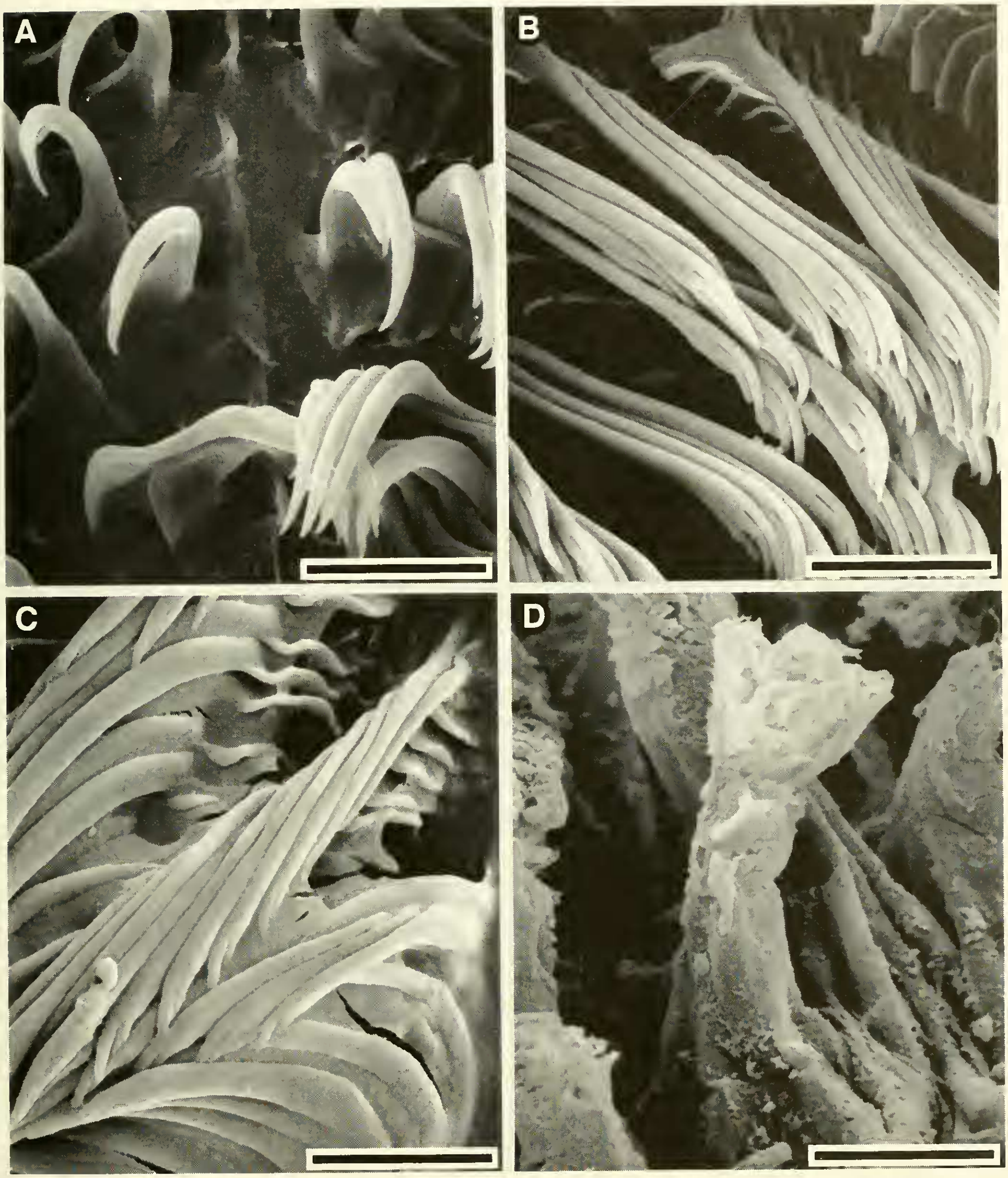

FIG. 40. *Rostanga ankyra,* new species, holotype. A. Inner lateral teeth; scale bar = 15 µm. B. Mid-lateral teeth; scale bar = 25 µm. C. Outer lateral teeth; scale bar = 20 µm. D, Caryophyllidium; scale bar = 43 µm.

the placement of this species in the genus *Rostanga.*

Rudman & Avern (1989) revised the genus *Rostanga* in the Indo-West Pacific. According to these authors there are nine valid species in this region, all of them characterized by a red or orange general color. More recently, Garovoy et al. (in press) described three new species from South Africa, and included *Boreodoris setidens* Odhner, 1939, in the genus *Rostanga. Rostanga setidens,* as well as one of the new species from South Africa, have a white background color. However, the new species from South Africa is clearly distinguishable from *R. ankyra* in having the dorsum covered with purplish brown spots (Garovoy et

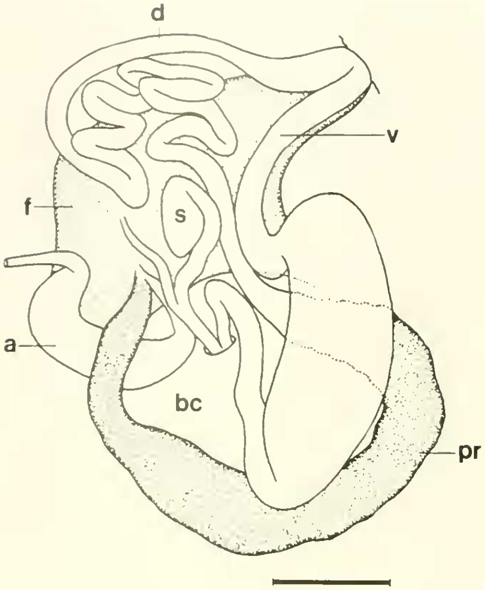

FIG. 41. *Rostanga ankyra*, new species, holotype. Reproductive system. Abbreviations: a, ampulla; bc, bursa copulatrix; d, deferent duct; f, female glands; pr, prostate; s, seminal receptacle; v, vagina.

al., in press). Other differences include the presence of jaw elements, and the lack of denticles on the mid-lateral teeth of the new species from South Africa. *Rostanga setidens*, on the other hand, has a radular morphology very similar to *R. ankyra*, and both species lack jaws. The main radular difference is the presence of a single denticle in all the lateral teeth of *R. setidens* (see Odhner, 1939), whereas in the mid-lateral teeth of *R. ankyra* there are two long denticles. The reproductive system of *R. ankyra* has a very long deferent duct, and a wide, muscular portion in the vagina, whereas in *R. setidens* the deferent duct is shorter, and the vagina is simple.

Genus *Sclerodoris* Eliot, 1904

Type Species: *Sclerodoris tuberculata* Eliot, 1904, by subsequent designation herein.

Sclerodoris virgulata Valdés, new species (Figs. 29G, 42, 43)

Material Examined

HOLOTYPE: South of New Caledonia, Chalcal 2 Expedition, stn. CP27 (23°15′S, 168°05′E), 283 m, 31 October 1985, 14 mm preserved length, leg. P. Bouchet, B. Métivier and B. Richer de Forges (MNHN).

PARATYPES: South of New Caledonia, Chalcal 2 Expedition, stn. CP27 (23°15′S, 168°05′E), 283 m, 31 October 1985, one specimen 12 mm preserved length, leg. P. Bouchet, B. Métivier and B. Richer de Forges (CASIZ 121100). Norfolk Ridge, New Caledonia, Bathus 3 Expedition, stn. CP847 (23°03′S, 166°58′E), 405–411 m, 1 December 1993, one specimen 10 mm preserved length, leg. P. Bouchet, B. Richer de Forges and A. Warén (MNHN).

External Morphology

The body is elevated and oval (Fig. 29G). The dorsum is covered with long, thin caryophyllidia, the largest reaching over 100 μm (Fig. 42D). They have a small ciliated tubercle and 4–5 spicules around it. There are no dorsal ridges or depressions. The perfoliate rhinophores are composed of 21 lamellae. There are four long, thin, bipinnate branchial leaves. Ventrally, the oral tentacles are short and conical (Fig. 43E). The anterior border of the foot is notched and grooved. The mantle margin is about as wide as the foot.

The color of the living animals is white, with a series of dark brown spots and lines. These spots and lines are arranged in a regular pattern. There are numerous spots in the center of the dorsum that in two specimens may line up to form a line, running from the rhinophores to the gill. Along the mantle margin there are several lines projecting radially from the center of the dorsum. There are small spots distributed irregularly among the central and radial lines. The rhinophores and gill are also white.

Anatomy

The posterior end of the oral tube has six strong retractor muscles (Fig. 43C), which are attached to the body wall. The oval, muscular buccal bulb has two additional muscles. The buccal bulb is about as long as the oral tube. The labial cuticle is smooth. The radular formula is 31 × (41.0.41) in a 10 mm preserved length specimen. There are no rachidian teeth. The inner lateral teeth are hamate, having a single cusp, and they lack denticles (Fig. 42A). The teeth increase in size suddenly towards the medial portion of the half-row. The mid-lateral teeth are also hamate and lack denticles

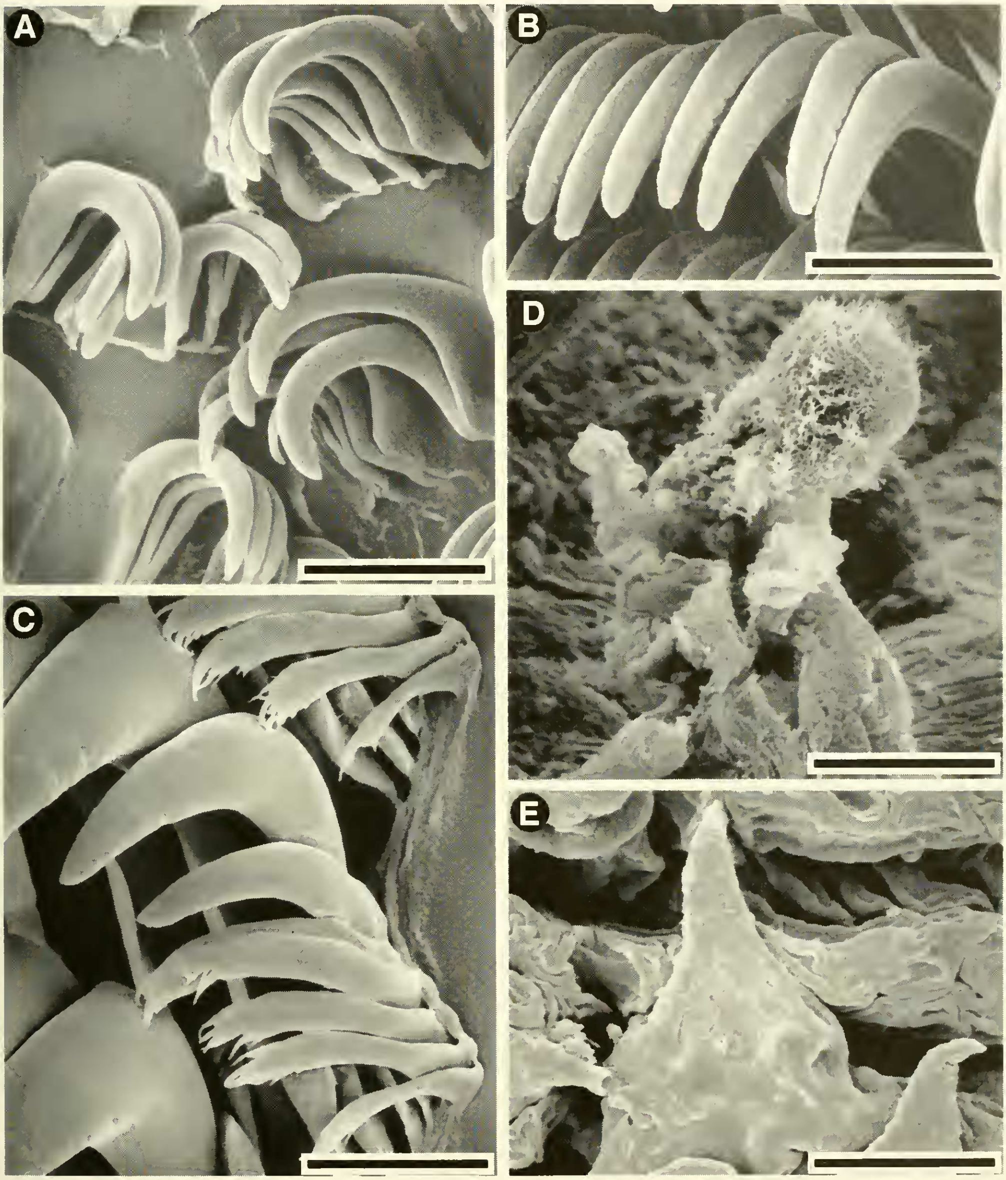

FIG. 42. *Sclerodoris virgulata,* new species, paratype from Bathus 3 (stn. CP847). A. Inner lateral teeth; scale bar = 25 µm. B. Mid-lateral teeth; scale bar = 43 µm. C. Outer lateral teeth; scale bar = 30 µm. D. Caryophyllidium; scale bar = 30 µm. E. Penial hooks; scale bar = 43 µm.

(Fig. 42B). The outermost teeth are elongate, with a short base, and have 3–11 long denticles (Fig. 42C). The esophagus is long and connects directly to the stomach (Fig. 43A).

The ampulla is long; it narrows into the gonoduct, which branches into a short oviduct and the prostate (Fig. 43B). The oviduct enters the female glands near the nidamental opening. The prostate is flattened and granular; it is divided into two portions that are clearly distinguishable by their different texture and coloration. The deferent duct is long and narrow; it opens into a common, large atrium with the vagina. The penis is armed

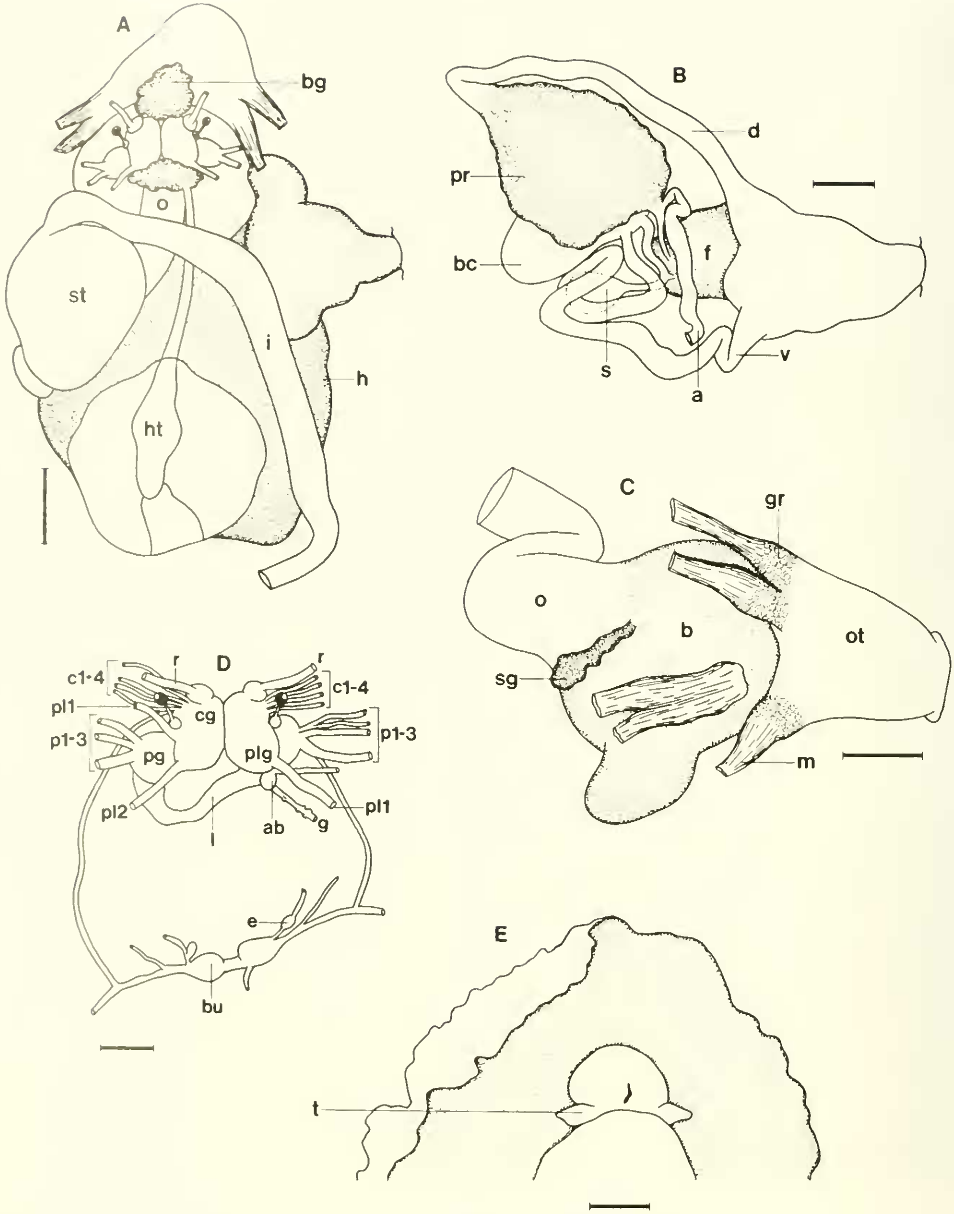

FIG. 43. *Sclerodoris virgulata,* new species, paratype from Bathus 3 (stn. CP847). A. Dorsal view of the anatomy; scale bar = 0.5 mm. B. Reproductive system; scale bar = 0.25 mm. C. Anterior portion of the digestive system; scale bar = 0.5 mm. D. Central nervous system; scale bar = 0.25 mm. E. Mouth area; scale bar = 0.5 mm. Abbreviations: a, ampulla; ab, abdominal ganglion; b, buccal bulb; bc, bursa copulatrix; bg, blood gland; bu, buccal ganglion; c, cerebral nerve; cg, cerebral ganglion; d, deferent duct; e, esophageal ganglion; f, female glands; g, genital nerve; gr, glandular region of the retractor muscles; h, hermaphrodite and digestive glands; ht, heart; i, intestine; l, visceral loop; m, retractor muscle; o, esophagus; ot, oral tube; p, pedal nerve; pg, pedal ganglion; pl, pleural nerve; plg, pleural ganglion; pr, prostate; r, rhinophoral nerve; s, seminal receptacle; sg, salivary gland; st, stomach; t, oral tentacle; v, vagina.

with large, triangular hooks, about 70 µm long (Fig. 42E). The vagina is very long; at its proximal end, it connects to the large and irregular bursa copulatrix. From the bursa copulatrix leads another long duct that connects to the seminal receptacle and the very short uterine duct. The bursa copulatrix is about ten times larger than the seminal receptacle.

In the central nervous system (Fig. 43D), the cerebral and pleural ganglia are fused and distinct from the pedal ganglia. There are four cerebral nerves leading from each cerebral ganglion, and two (left) or one (right) pleural nerves lead from the pleural ganglion. The buccal ganglia lie near the rest of the central nervous system, joined to the cerebral ganglia by two long nerves. Gastroesophageal, rhinophoral, and optical ganglia are present. The pedal ganglia are clearly separated, having three nerves leading from each one. The pedal and parapedal commissures are enveloped together with the visceral loop along all their length. There is an abdominal ganglia on the right side of the visceral loop.

The circulatory system (Fig. 43A) consists of a heart and two blood gland situated in front and behind the central nervous system.

Etymology

From the Latin *virgulatus* (striped), in reference to the numerous black lines on the dorsum of this species.

Remarks

Rudman (1978) revised the genus *Sclerodoris* in the Indo-West Pacific. He recognized eight valid species in this area (two of them unnamed), all of them very different from *Sclerodoris virgulata.* All the species previously described have either dorsal ridges or depressions, which are absent in *S. virgulata.* Moreover, the combination of the following characters makes *S. virgulata* very easily distinguishable from other members of the genus: white color pattern with radial dark brown lines, absence of an accessory gland, caryophyllidia lacking a projecting filament, and presence of four, thin branchial leaves.

Another genus with caryophyllidia and denticulated outermost teeth is *Taringa* (Valdés & Gosliner, in press). However, *S. virgulata* does not fit in *Taringa* in having penial hooks and lacking a cuticular structure in the penis. In addition, *Taringa* has the inner and mid-lateral teeth denticulated, whereas they are smooth in *S. virgulata.*

Genus *Baptodoris* Bergh, 1884

Type Species: *Baptodoris cinnabarina* Bergh, 1884, by monotypy.

Baptodoris phinei Valdés, new species

(Figs. 29D, 44, 45)

Material Examined

HOLOTYPE: Coral Sea, Musorstom 5 Expedition, stn. 324 (21°15′S, 157°51′E), 970 m, 21 mm preserved length, leg. P. Bouchet, B. Métivier and B. Richer de Forges (MNHN).

External Morphology

The body is elevated and oval (Fig. 29D). The dorsum is covered with conical caryophyllidia, the largest reaching over 100 µm (Fig. 44D). They have a large, elongate ciliated tubercle and five spicules around it. The perfoliate rhinophores are composed of 32 lamellae. There are five tripinnate branchial leaves. The rhinophoral and branchial sheaths are low. Ventrally, the oral tentacles are short and conical. The anterior border of the foot is notched and grooved (Fig. 45E). The mantle margin is narrower than the foot.

The color of the living animal is uniformly white. The rhinophores and gill are also white.

Anatomy

The posterior end of the oral tube has six retractor muscles (Fig. 45C), which are attached to the body wall. The oval, muscular buccal bulb has two additional muscles. The buccal bulb is about as long as the oral tube. The labial cuticle is smooth. The radular formula is 20 × (18.0.18) in a 21 mm preserved length specimen. There are no rachidian teeth. The inner lateral teeth are hamate, having a single cusp with a large, rounded denticle (Fig. 44A). The teeth are very elongate with a short, strong cusp. The teeth increase in size gradually towards the medial portion of the half-row (Fig. 44A, B). The outermost teeth are short and have several, very small denticles (Fig. 44C). The esophagus is very long and wide, and connects directly to the stomach.

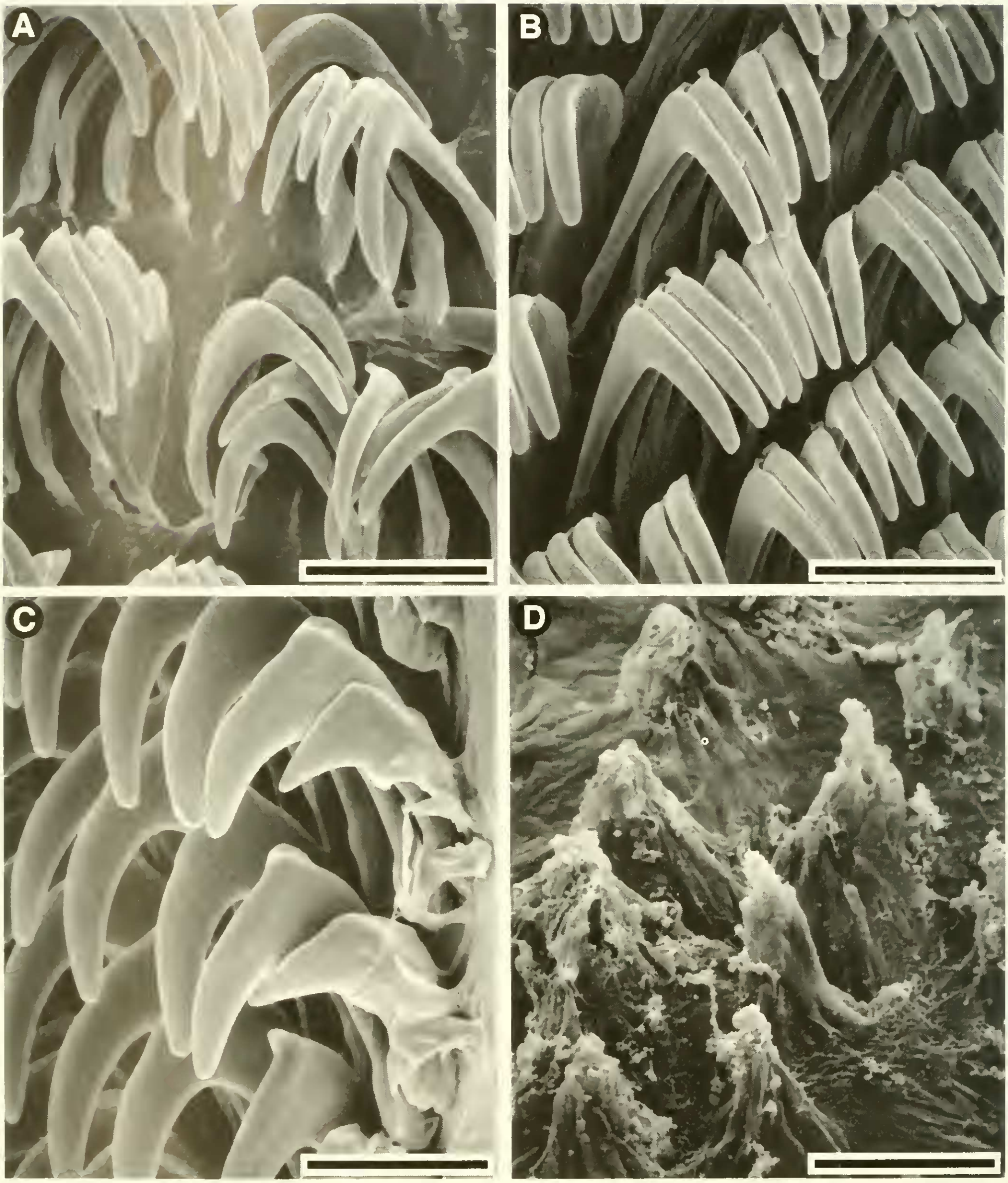

FIG. 44. *Baptodoris phinei,* new species, holotype. A. Inner lateral teeth; scale bar = 43 μm. B. Mid-lateral teeth; scale bar = 60 μm. C. Outer lateral teeth; scale bar = 75 μm. D. Caryophyllidia; scale bar = 150 μm.

The ampulla is long and convoluted; it narrows into the gonoduct, which branches into the short oviduct and the prostate (Fig. 45B). The oviduct enters the female glands near the nidamental opening. The prostate is large and granular; it is divided into two portions that are clearly distinguishable by their different texture and coloration; the largest portion is pale yellow and connects to the deferent duct, whereas the smallest portion is orange and connects to the ampulla. The deferent duct is long and narrow; it expands into the ejaculatory portion, which opens into a common atrium with the vagina. The penis is unarmed. There is a simple accessory gland that opens into the atrium, between the deferent duct and

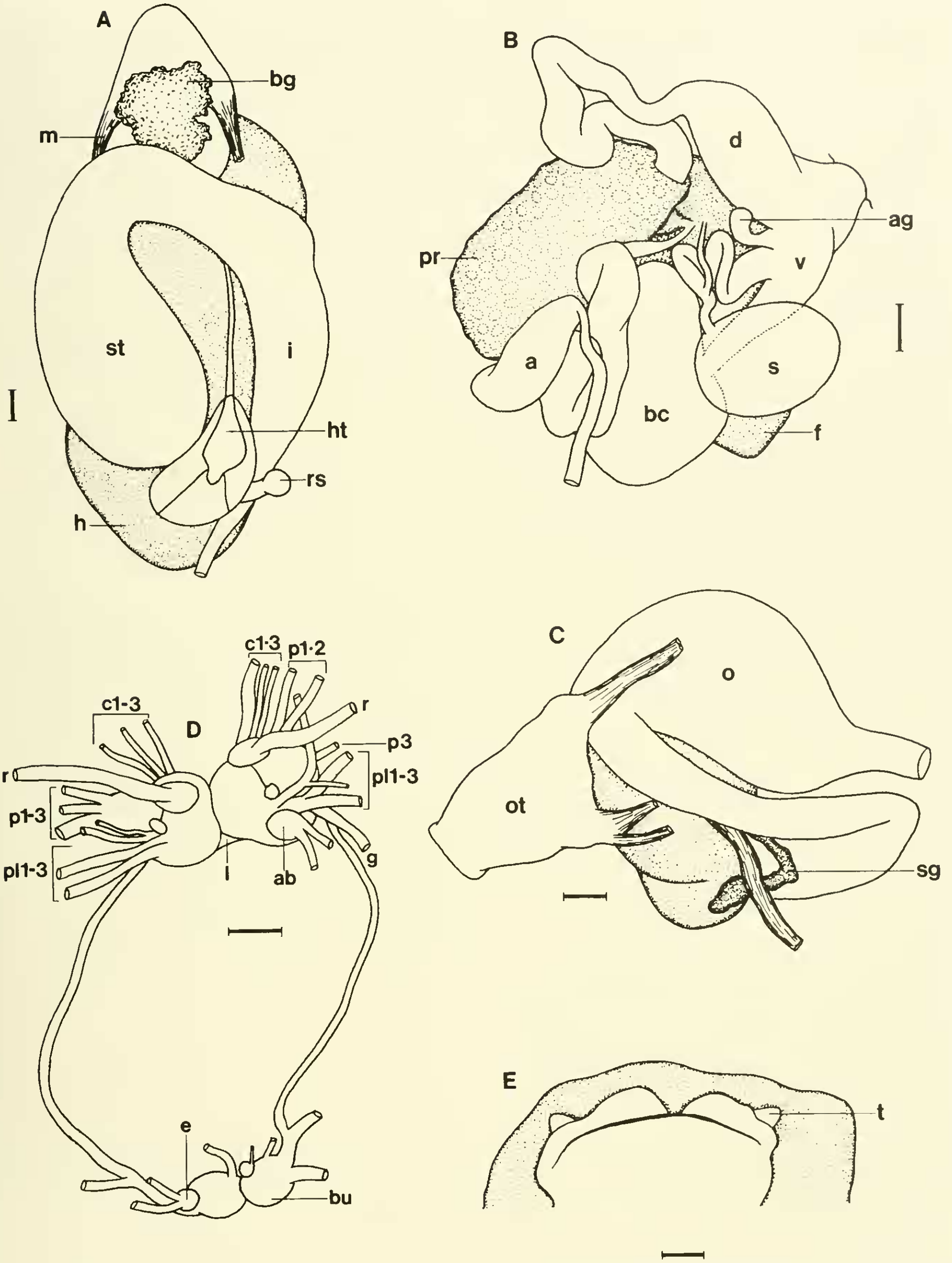

FIG. 45. *Baptodoris phinei*, new species, holotype. A. Dorsal view of the anatomy; scale bar = 1 mm. B. Reproductive system; scale bar = 1 mm. C. Anterior portion of the digestive system; scale bar = 1 mm. D. Central nervous system; scale bar = 0.5 mm. E. Mouth area; scale bar = 1 mm. Abbreviations: a, ampulla; ab, abdominal ganglion; ag, accessory gland; b, buccal bulb; bc, bursa copulatrix; bg, blood gland; bu, buccal ganglion; c, cerebral nerve; d, deferent duct; e, esophageal ganglion; f, female glands; g, genital nerve; h, hermaphrodite and digestive glands; ht, heart; i, intestine; 1, visceral loop; m, retractor muscle; o, esophagus; ot, oral tube; p, pedal nerve; pl, pleural nerve; pr, prostate; r, rhinophoral nerve; rs, renal syrinx; s, seminal receptacle; sg, salivary gland; st, stomach; t, oral tentacle; v, vagina.

the vagina. The vagina is short; at its proximal end, it connects to the large, oval bursa copulatrix. From the distal portion of the vagina leads another long duct that connects to the seminal receptacle and the uterine duct. The bursa copulatrix is about twice as large as the seminal receptacle.

In the central nervous system (Fig. 45D), the cerebral and pleural ganglia are fused and distinct from the pedal ganglia. There are three cerebral nerves leading from each cerebral ganglion, and three pleural nerves lead from each pleural ganglion. The buccal ganglia lie near the rest of the central nervous system, joined to the cerebral ganglia by two long nerves. Gastroesophageal, rhinophoral and optical ganglia are present. There are no eyes. The pedal ganglia are clearly separated, having three nerves leading from each. A large abdominal ganglion lies on the right side of the central nervous system. The pedal and parapedal commissures are enveloped together with the visceral loop along all their length.

The circulatory system (Fig. 45A) consists of a heart and a single blood gland situated over the central nervous system.

Etymology

Dedicated to Phineus, the mythical prophet who was blinded by Zeus, in reference to the lack of eyes of this species.

Remarks

The genus *Baptodoris* was recently diagnosed by Valdés & Gosliner (in press) as having the dorsum covered with caryophyllidia, prostate with two portions, penis armed with hooks, and a gap without hooks near the opening, accessory gland lobate, without a spine, labial cuticle smooth, and outermost lateral teeth very small and multidenticulate. *Baptodoris phinei* has all these characteristics except for the penial hooks. However, *B. phinei* share more features with members of the *Baptodoris* clade than with other caryophyllidia-bearing dorids and therefore it is provisionally placed in this genus. Also, *B. phinei* share with one of the two valid species of the genus, *Baptodoris cinnabarina* Bergh, 1884, the presence of a single, large denticle on the cusp of the lateral radular teeth.

Baptodoris phinei is clearly distinguishable from the two other members of the genus *Baptodoris* by the external morphology and anatomy. *Baptodoris cinnabarina* is yellow to dark red with white and brown spots (Valdés & Gosliner, in press), and *B. mimetica* Gosliner, 1991, is bright lemon yellow with white spots (Gosliner, 1991), whereas *P. phinei* is uniformly pale cream. The anatomical unique features of *P. phinei* are the lack of eyes and the absence of penial hooks.

Genus *Dendrodoris* Ehrenberg, 1831

Type Species: *Dendrodoris lugubris* Ehrenberg, 1831, by subsequent designation by Gray (1847).

Dendrodoris orbicularis Valdés, new species (Figs. 29F, 46)

Material Examined

HOLOTYPE: Southeast of New Caledonia, Halipro 1 Expedition, stn. CC856 (21°44′S, 166°37′E), 311–365 m, 20 March 1994, 47 mm preserved length, dissected, leg. B. Richer de Forges (MNHN).

PARATYPES: New Caledonia, Musorstom 4 Expedition, stn. CP135 (18°55′S, 163°22′E), 456 m, 19 September 1985, one specimen 46 mm preserved length, dissected, leg. P. Bouchet and B. Richer de Forges (MNHN). Southeast of New Caledonia, Halipro 1 Expedition, stn. CC851 (21°43′S, 166°37′E), 314–364 m, 19 March 1994, one specimen 14 mm preserved length, dissected, leg. B. Richer de Forges (MNHN). North of New Caledonia, Bathus 4 Expedition, stn. CP906 (19°01′S, 163°15′E), 339–350 m, 4 September 1994, one specimen 20 mm preserved length, dissected, leg. B. Métivier and B. Richer de Forges (CASIZ 121101); stn. DW925 (18°55′S, 163°24′E), 370–405 m, 7 August 1994, one specimen 11 mm preserved length, dissected, leg. B. Métivier and B. Richer de Forges (MNHN).

External Morphology

The body is elevated, oval (Fig. 29F), soft in texture. The dorsum is smooth, lacking tubercles. The perfoliate rhinophores consist of 37 lamellae. There are six tripinnate branchial leaves. Ventrally there are no oral tentacles. The anterior border of the foot has a deep notch where the mouth opens (Fig. 46E). The

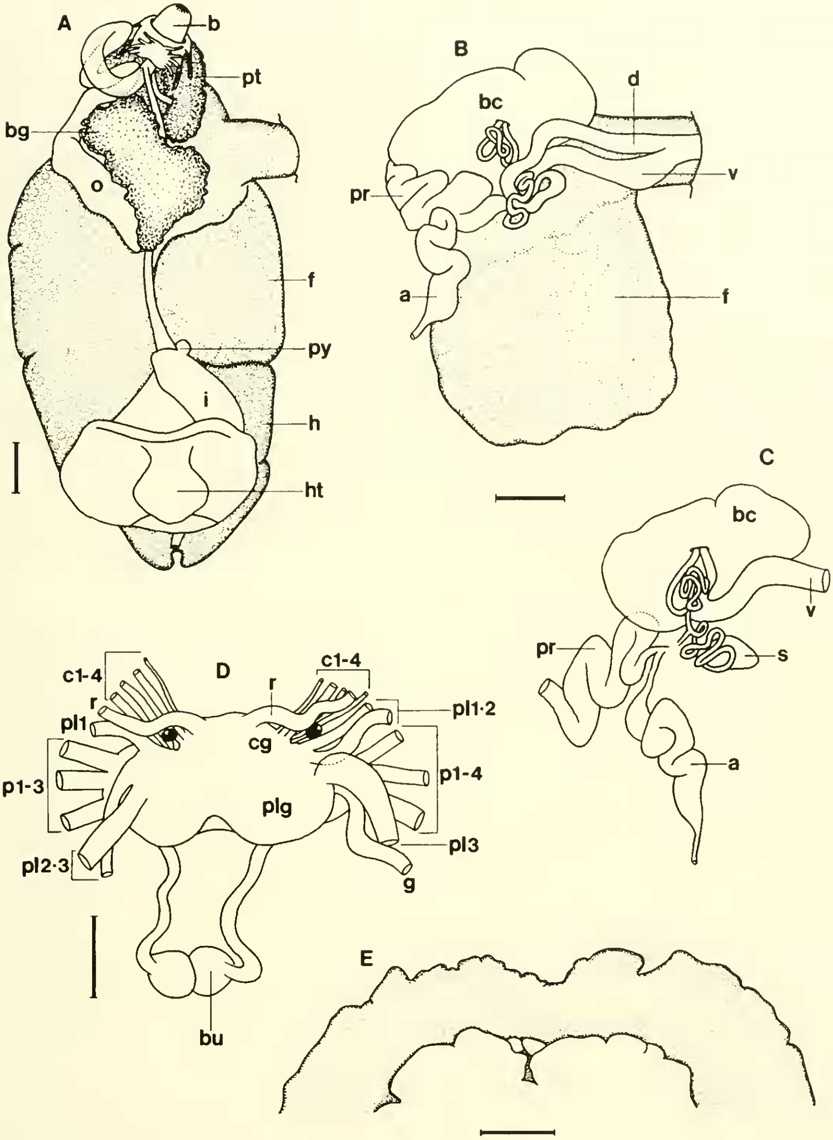

FIG. 46. *Dendrodoris orbicularis,* new species, paratype from Musorstom 4 (stn. CP135). A. Dorsal view of the anatomy; scale bar = 2 mm. B. Reproductive system; scale bar = 2 mm. C. Detail of several reproductive organs; scale bar = 2 mm. D. Central nervous system; scale bar = 1 mm. E. Mouth area; scale bar = 3 mm. Abbreviations: a, ampulla; b, buccal bulb; bc, bursa copulatrix; bg, blood gland; bu, buccal ganglion; c, cerebral nerve; cg, cerebral ganglion; d, deferent duct; f, female glands; g, genital nerve; h, hermaphrodite and digestive glands; ht, heart; i, intestine; o, esophagus; p, pedal nerve; pl, pleural nerve; plg, pleural ganglion; pr, prostate; pt, ptyaline gland; py, pyloric sac; r, rhinophoral nerve; s, seminal receptacle; v, vagina.

foot is very wide, almost ten times wider than the mantle margin

The color of the living animals is unknown. Only one specimen, the holotype, retained some of the original coloration. It is pale brown with several, large rings of dark brown. The interior of some ridges is darker than the rest of the dorsum. The mantle margin is edged by a thin, white line, that is interiorly surrounded by a wider black band. Ventrally, there are faded brown spots densely distributed on the foot sole, and a few, larger scattered on the mantle margin. The other specimens are uniformly cream, some of them with faded patches of dark brown.

Anatomy

The posterior end of the buccal bulb has four thin retractor muscles (Fig. 46A), which attach to the body wall. There are no salivary glands. Two large ptyaline glands are joined together to a single duct that opens into the buccal bulb. There are no jaws and radula. The esophagus is long and convoluted. It has two rounded esophageal glands and connects directly to the digestive gland. The intestine is short and has a pyloric sac on its proximal region (Fig. 46A).

The ampulla is long and convoluted; it narrows into the gonoduct, which branches into a short oviduct and the prostate (Fig. 46C). The oviduct enters the female glands near the center of the mass. The prostate is tubular, granular, and elongate (Fig. 46B); it narrows and expands again into the long deferent duct. The deferent duct opens into a common atrium with the vagina. The penis is unarmed. The vagina is long and wide; at its proximal end, it connects to the large, irregular bursa copulatrix. Another very long, convoluted duct, which connects to the seminal receptacle and to the short uterine duct, leads from the bursa copulatrix. The bursa copulatrix is about twenty times larger than the seminal receptacle.

In the central nervous system (Fig. 46D), the cerebral and pleural ganglia are fused and distinct from the pedal ganglia. There are four cerebral nerves leading from each cerebral ganglion, and three pleural nerves lead from each pleural ganglion. The buccal ganglia lie near the rest of the central nervous system, joined to the cerebral ganglia by two short nerves. Optical ganglia are present. The rhinophoral ganglia appear to be fused with the cerebral ganglia. The two pedal ganglia are joined together ventrally, having three nerves leading from each one. There are no pedal and parapedal commissures.

The circulatory system (Fig. 46A) consists of a heart and a single blood gland situated behind the central nervous system.

Etymology

From the Latin *orbis* (circle, ring), in reference to the brown rings on the dorsum of this species.

Remarks

Dendrodoris orbicularis is easily distinguishable from other Indo-Pacific species of *Dendrodoris* by its external coloration. There are no other species described from this area with a color pattern of large, dark dorsal rings.

In addition, the lack of penial hooks in *D. orbicularis* differentiates this species from most of the others studied anatomically. Only *Dendrodoris coronata* Kay & Young, 1969, also lacks penial hooks too (Kay & Young, 1969; Valdés & Gosliner, 1999), but this species is easily distinguished from *D. orbicularis* in having a white coloration with black spots, dorsal tubercles, the seminal receptacle larger than the bursa copulatrix and a very short ampulla (Valdés & Gosliner, 1999).

Dendrodoris brodieae Valdés, new species
(Figs. 13D, 47A, B, 48A)

Material Examined

HOLOTYPE: North of New Caledonia, Musorstom 4 Expedition, stn. CP153 (19°04′S, 163°21′E), 235 m, 14 September 1985, one specimen 14 mm preserved length, leg. P. Bouchet and B. Richer de Forges (MNHN).

PARATYPES: South of New Caledonia, Musorstom 4 Expedition, stn. DW227 (22°46′S, 167°20′E), 300 m, 30 September 1985, one specimen 19 mm preserved length, leg. P. Bouchet and B. Richer de Forges (CASIZ 121102). South of New Caledonia, Chalcal 2 Expedition, stn. DW81 (23°20′S, 168°03′E), 311 m, 31 October 1986, one specimen 31 mm preserved length, dissected, leg. P. Bouchet, B. Métivier, B. Richer de Forges (MNHN).

External Morphology

The body of the living animal is elevated, oval, soft in texture (Fig. 13D). The dorsum is smooth, lacking tubercles. The perfoliate rhinophores consist of 32 lamellae. There are six tripinnate branchial leaves. Ventrally there are no oral tentacles. The anterior border of the foot has a deep notch where the mouth opens. The foot is very wide, almost ten times wider than the mantle margin.

The general color of the body is pale brown. The dorsum is covered with numerous, rounded or oval pale cream spots. Among them, there are several large, dark brown patches. In some cases, the brown patches

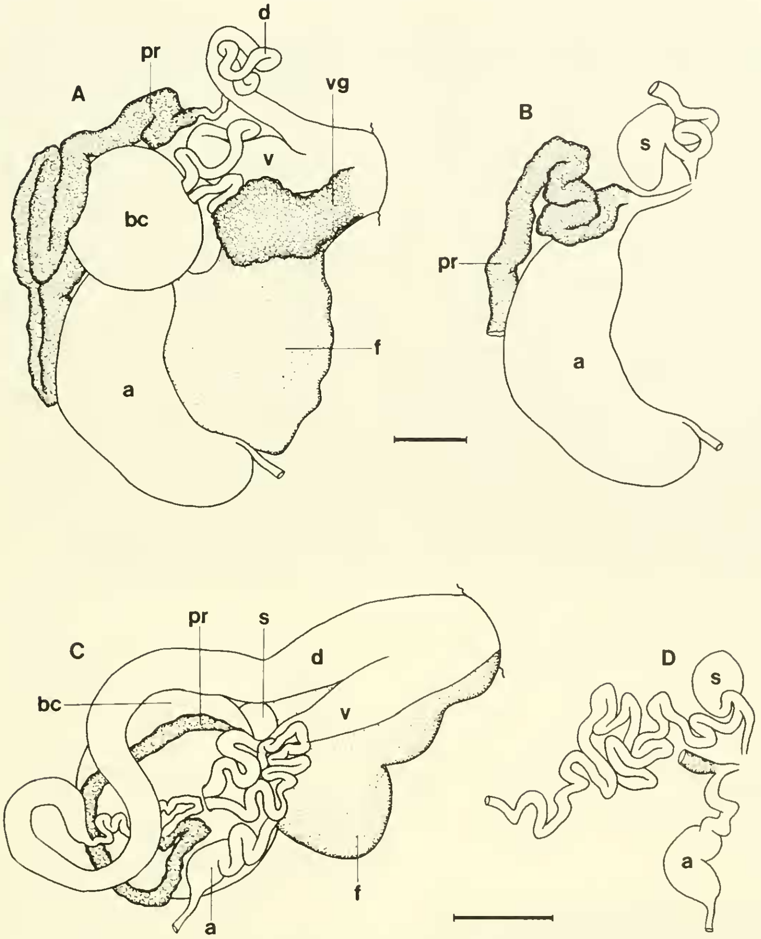

FIG. 47. Reproductive systems. A, B. *Dendrodoris brodieae,* specimen from Chalcal 2 (DW81); scale bar = 1 mm. C, D. *Dendrodoris* sp., specimen from Musorstom 3 (stn. CP110); scale bar = 1 mm. Abbreviations: a, ampulla; bc, bursa copulatrix; d, deferent duct; f, female glands; pr, prostate; s, seminal receptacle; v, vagina; vg, vestibular gland.

overlap the white spots. The mantle edge is surrounded by a white or pale cream line, interrupted by dark brown, almost black spots. These spots are connected to pale brown spots situated on the mantle margin. The rhinophores are cream with the apex black. The gill is also cream with the lamellae edged with dark brown pigment.

Anatomy

The reproductive system has a wide, simple ampulla; it narrows into the gonoduct, which branches into a long oviduct and the prostate (Fig. 47B). The oviduct enters the female glands near the center of the mass. The prostate is tubular, granular and elongate (Fig. 47A); it narrows and expands again into the deferent duct. The deferent duct opens into a common atrium with the vagina. The penis is armed with several rows of elongate hooks. The hooks have long bases and conical cusps, about 50 µm long (Fig. 48A). The vagina is long and wide; at its proximal end, it connects to the large and rounded bursa copulatrix. Another long, convoluted duct, which connects to the seminal receptacle and to the short uterine duct, leads from the bursa copulatrix. The bursa copulatrix is about ten times larger than the seminal receptacle.

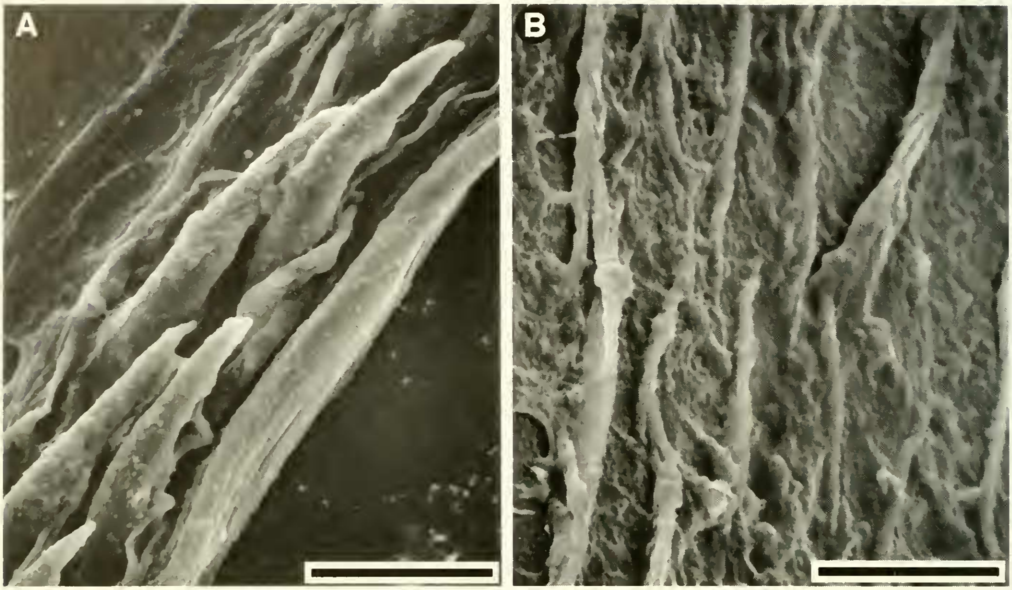

FIG. 48. Penial hooks. A. *Dendrodoris brodieae*, specimen from Chalcal 2 (DW81); scale bar = 25 µm. B. *Dendrodoris* sp., specimen from Musorstom 3 (stn. CP110); scale bar = 20 µm.

Etymology

Dedicated to Gilianne Brodie, who is reviewing the genus *Dendrodoris* in the Indo-West Pacific

Remarks

Dendrodoris brodieae is clearly distinguishable from other Indo-Pacific species of *Dendrodoris* by its external coloration. The only other species with cream rounded spots on the dorsum is *Dendrodoris guttata* (Odhner, 1917). However, *D. guttata* has also black spots in the middle of the cream spots (Willan & Coleman, 1984), which are absent in *D. brodieae*. In addition, *D. guttata* has a fawn or apricot general color, whereas *D. brodieae* is pale brown. Also, the dark brown spots of *D. brodieae* are absent in *D. guttata* (Willan & Coleman, 1984). *Dendrodoris denisoni* (Angas, 1864) also resembles *D. brodieae* in the external coloration, but these two species are clearly distinguishable by the presence of large tubercles in the former.

Internally, *D. brodieae* is characterized by having a very large vestibular gland. Other species of *Dendrodoris* with vestibular glands are *D. nigra* (Stimpson, 1855), *D. denisoni* (Angas, 1864), and *D. albobrunnea* Allan, 1933 (Brodie et al., 1997; Valdés & Gosliner, 1999). In *D. nigra* and *D. denisoni,* the vestibular gland is much smaller than that of *D. brodieae*. Only in *D. albobrunnea* it has a very large vestibular gland, comparable to that of *D. brodieae*. However, both species are distinguishable by the external morphology. *Dendrodoris albobrunnea* has small dorsal tubercles, whereas *D. brodieae* has a smooth dorsum. Moreover, *D. albobrunnea* is a very pale species with small brown spots, whereas *D. brodieae* has a much more complex coloration, with brown patches and pale cream spots.

Dendrodoris sp. (Figs. 47C, D, 48B)

Material Examined

Philippines, Musorstom 3 Expedition, stn. CP110 (14°00′N, 120°18′E), 187–193 m, 2 June 1985, one specimen 27 mm preserved length, dissected, leg. P. Bouchet and M. P. Triclot (MNHN).

External Morphology

The body is elevated, oval, soft in texture. The dorsum is smooth, lacking tubercles. The perfoliate rhinophores consist of 31 lamellae. There are six tripinnate branchial leaves. Ventrally there are no oral tentacles. The anterior border of the foot has a deep notch where the mouth opens. The foot is very wide, almost ten times wider than the mantle margin. The color of the living animal is unknown.

Anatomy

The reproductive system has a small, convoluted ampulla; it narrows into the gonoduct, which branches into a short oviduct and the prostate (Fig. 47D). The oviduct enters the female glands near the center of the mass. The prostate is tubular, granular and elongate (Fig. 47C); it narrows and expands again into the long and wide deferent duct. The deferent duct opens into a common atrium with the vagina. The penis is armed with several rows of penial hooks. The hooks have long bases and minute, rounded cusps, about 2 μm long (Fig. 48B). The vagina is long and wide; at its proximal end, it connects to the large and rounded bursa copulatrix. Another very long and convoluted duct, which connects to the seminal receptacle and to the short uterine duct, leads from the bursa copulatrix. The bursa copulatrix is about 20 times larger than the seminal receptacle.

Remarks

The penial hooks of this species appear to be very distinctive. However, a single specimen of this species was collected, and there is not information on the external coloration of the living animal. Therefore, I prefer not to name this likely new species before more material becomes available.

DISCUSSION

The deep-water species of cryptobranch dorids described in this paper have been compared with their known closest relatives inhabiting shallow waters. The anatomy and the generic placement of many shallow-water species of cryptobranch dorids from the tropical Indo-Pacific are poorly known. It may be possible that some of the tropical shallow-water species have large bathymetric ranges, showing a pale or white coloration when they occur in deep waters. For example, the notaspidean opisthobranch *Umbraculum umbraculum* Lightfoot, 1786, is found in eastern Australia from the intertidal zone to 274 m, and the deep-water specimens are translucent white, apparently lacking pigment (Rudman, 1999). However, most of the species described in the present paper, closest relatives of which have been anatomically studied, show notable anatomical differences from the shallow-water species and they clearly constitute new species. Moreover, the evidence indicates that most species of cryptobranch dorids have, in general, narrow bathymetric ranges. As for the phyllidiids on the Norfolk Ridge (Valdés, 2001), the present material shows that several deep-sea assemblages replace each other in different depth zones. For instance, of the ten species found in the 200–400-m depth interval, one (*Cadlina abyssicola*) has been recorded from deeper than 500 m and another (*Pharodoris diaphora*) from more shallow than 100 m. Conversely, of the seven species found in the 500–1,000-m interval, only two (*Cadlina abyssicola* and *Discodoris achroma*) are recorded from shallower depths than 500 m. Even if only species represented by more than one lot are considered, there is evidence for a considerable species turnover: of the five species found at more than one station in the 200–400-m depth interval, one (*Cadlina abyssicola*) has been recorded from deeper than 500 m and another (*Pharodoris diaphora*) from more shallow than 100 m. Conversely, of the five species found at more than one station in the 500–1000-m interval, two (*Cadlina abyssicola* and *Discodoris achroma*) have been recorded from more shallow than 500 m.

The species studied in this paper belong to 13 genera of cryptobranch dorids. Most of these genera—*Cadlina, Geitodoris, Discodoris, Peltodoris, Paradoris, Diaulula, Rostanga, Sclerodoris* and *Dendrodoris*—are here reported from deep waters for the first time, and two, *Goslineria* and *Pharodoris,* are here described. Some of these genera are more commonly found in cold or temperate waters. *Austrodoris* has been reported from Antarctic cold Atlantic waters (Bouchet, 1977; Wägele, 1990), *Cadlina* has been found in cold and temperate waters of Antarctica, South America, Japan, North America, Europe and South Africa (Rudman, 1984; Gosliner, 1987b), and *Diaulula,* which has only one species assigned with certainty, was described from cold or temperate waters in the Americas and Japan (McDonald, 1983). Other genera, such as *Rostanga, Paradoris, Geitodoris* and *Baptodoris,* are widespread and are not commonly found in cold regions (Baba, 1986; Rudman & Avern, 1989; Gosliner, 1991;

Miller, 1995, 1996; Ortea, 1995). Finally, only two genera, *Sclerodoris* and *Dendrodoris,* are strictly from tropical or subtropical areas (Rudman, 1978; Valdés & Gosliner, 1999).

Several hypotheses could explain the presence of both tropical and cold water species in Indo-Pacific deep waters. Species of *Austrodoris,* which are absent from the tropical Indo-Pacific, are likely related to the Antarctic species. *A. kerguelenensis,* also found in New Caledonia *Austrodoris kerguelenensis* also occurs in the Antarctic deep-sea, and has a very wide geographic and bathymetric range (only in cold waters). Since the two other species found in New Caledonia share at least a portion of their geographic range with *A. kerguelenensis,* vicariance does not explain the process of speciation that took place in this area. The species of *Austrodoris* described here are found in deeper and therefore colder waters, from 500 to 1,300 m depth, whereas the rest of the species, with the exception of *Baptodoris phinei,* were collected in shallower areas. It appears that *Austrodoris* is better adapted to cold waters than other genera and this genus occurs in large numbers in the Antarctic (Wägele, 1990) and the tropical deep sea. The tropical deep sea could be a relict area where species of *Austrodoris* occurred since the early Pliocene. Gosliner (1987a) hypothesized that during the early Pliocene, when ocean temperatures began to drop, it is likely that many species of marine organisms were widely distributed throughout the southern oceans. The oceanic warming during portions of the Pleistocene could have served as an extinction mechanism of these cold-water species in large areas of their geographic ranges. The deep-water environment could have served as a refuge where *Austrodoris* species survived.

On the other hand, most of the genera found in deep waters are not present in the Antarctica. In the case of *Sclerodoris* and *Dendrodoris,* the species found in New Caledonia must have tropical sister taxa, since these genera are strictly found in tropical waters. Vertical dispersal followed by subsequent vicariance could explain the presence of these tropical species in the deep sea. Members of *Sclerodoris* and *Dendrodoris* have always been found at 460 m or less, being among the species with a shallowest occurrence.

The genera *Rostanga, Paradoris, Cadlina* and *Geitodoris* have representatives in the temperate waters of New Zealand (Miller, 1980; Rudman & Avern, 1989; Miller, 1995, 1996), very close to New Caledonia, and it is possible that vicariant events were involved in the evolution of this species. Again, as Gosliner (1987a) hypothesized for South African species, the ocean warming during the Pleistocene could have served as an isolating mechanisms that resulted in speciation. Members of *Paradoris, Cadlina* and *Geitodoris* appear to be absent from the rest of the Indo-Pacific and also vicariance seems to be a likely explanation for the range of these species. Phylogenetic studies on each genus would determine the sister-group relationships and biogeographic patterns of the deep-water species here described.

Most of the species studied in this paper have a pale, simple external coloration. Many of them are uniformly pale cream or white, and only a few have two contrasting colors. Bouchet (1977) described several species from Atlantic deep waters with similar color patterns. Valdés (2001) found that species of *Phyllidiopsis* show certain correlation between their color and their collection depth. Species found deeper have simpler and paler color patterns. The coloration of shallow-water dorid nudibranchs is believed to have a strong defensive significance (Gosliner & Behrens, 1990). Several defensive systems based on color have been described in dorid nudibranchs, that included aposematic coloration and mimicry, but also crypsis and special resemblance. Due to the partial or total absence of light in deep waters, the coloration of deep-sea dwellers is probably not very useful in an interaction with potential predators. Therefore, deep-sea nudibranchs probably rely on other defensive systems, that are also present in shallow water species, for example, chemical defense and spicules (Avila, 1995). Chemical studies have not been carried out on deep-sea nudibranchs, to determine whether they may have higher concentrations of toxic chemicals than shallow waters species.

Since most deep-water dorids have a pale coloration, that must be some sort of ecological advantage for these animals. The most likely possibility is that deep-sea animals conserve energy by not producing pigments that they are not going to use. Also, pale colorations may help to camouflage species that inhabit moderately deep waters, where some light is still available.

Two of the species studied in this paper lack eyes, in what also seems to be another adaptation to living in deep waters. Other blind species of nudibranchs have been previously described from deep waters in the Arctic, Atlantic and Pacific Oceans (Wägele, 1989; Baranets, 1993; Valdés & Bouchet, 1998a, 1998b; Valdés & Bertsch, 2000). The blind species collected from New Caledonia are *Austrodoris caeca* and *Baptodoris phinei,* and both were collected at great depths, from 650 to 1,330 m in the case of the former and at 970 m in the latter. The rest of the species, which have well-developed eyes, were collected from areas shallower than 700 m depth. The blind Atlantic species previously described are from 1,685 and 2,538-3,016 m depth (Valdés & Bouchet, 1998a, 1998b).

For this paper, 23 species have been studied, of which 18 are from New Caledonia, four from the Philippines, three from Vanuatu, and one from Wallis and Futuna (the total does not add up to 23 because some species occur in more than one region). According to Philippe Bouchet (pers. comm.), New Caledonia has been sampled more extensively than any other place, and the number of records undoubtedly reflects this sampling effort more than actual differences in absolute species richness. It is noteworthy that nearly half of the total number (11 species) have been collected from the Norfolk Ridge alone, a site of complex topography with extensive hard bottoms.

Only three stations, all from New Caledonia, had more than one species (Bathus 1 sta. CP711: *Austrodoris labouteі, Pharodoris diaphora;* Bathus 3 sta. CP847: *Cadlina abyssicola, Sclerodoris virgulata;* and Halipro 1 sta. CP851: *Paradoris araneosa, Dendrodoris orbicularis*). This contrasts with the experience of opisthobranch collectors in tropical shallow water, where the syntopic co-occurrence of several species of cryptobranch dorids is not exceptional.

An indication that the deep-water fauna of cryptobranch dorids is still far from adequately inventoried is given by the fact that 14 species (61%) are represented by single specimens.

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